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EDITOR: STEPHEN L. WOOD

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LATE QUATERNARY PLANT ZONATION AND CLIMATE IN SOUTHEASTERN UTAH

Julio L. Betancourt[1]

Abstract.— Plant macrofossils from packrat middens in two southeastern Utah caves outline development of modern plant zonation from the late Wisconsin. Allen Canyon Cave (2195 m) and Fishmouth Cave (1585 m) are located along a continuous gradient of outcropping Navajo Sandstone that extends from the Abajo Mountains south to the San Juan River. By holding the site constant, changes in the floral composition for a plot of less than one hectare can be observed, even if sporadically, over tens of millennia. At Allen Canyon Cave, Engelmann spruce-alpine fir forest was replaced by the present vegetation consisting of pinyon-juniper woodland on exposed ridgetops and cliffside stands of Douglas fir, ponderosa pine, and aspen. Xerophytic woodland plants such as pinyon, plains prickly pear, and narrowleaf yucca arrived sometime in the middle Holocene between 7200 and 3400 B.P. At Fishmouth Cave, Utah juniper in Holocene middens replaced blue spruce, limber pine, Douglas fir, and dwarf and Rocky Mountain junipers in late Wisconsin samples.

Disharmonious associations for the late Wisconsin occur only at the lower site with the xerophytes Mormon tea, plains prickly pear, and narrowleaf yucca growing alongside subalpine conifers. One possible explanation involves the late Wisconsin absence of ponderosa and pinyon pines from the Colorado Plateaus. Released from competition at their lower limits, subalpine conifers were able to expand into lower elevations and mix with xerophytic plants found today in understories of pinyon-juniper and ponderosa pine woodlands. Quantitative climatic estimates are derived for the late Wisconsin by applying vertical gradients for temperature and precipitation to the amount of vegetation depression. The Fishmouth Cave sequence indicates a minimum lowering of 850 m for blue spruce, limber pine, and dwarf juniper. A depression of at least 700 m for Engelmann spruce and alpine fir is suggested for the Allen Canyon locality. Use of conservatively low gradients for stations below 2080 m yields a 3–4 C cooling from present mean annual temperature and 35 to 60 percent more rainfall than today. Steeper gradients associated with more mountainous terrain suggest a 5 C lowering in temperature and up to 120 percent increase over modern precipitation.

Elevational plant zonation is by tradition the interpretative framework used in paleobotanical studies of the Southwestern United States. Early emphasis was placed on the amount of lowering for vegetation zones during Wisconsin cooling. Pollen studies such as that by Maher (1963) focused on upper treeline movement in the San Juan Mountains, and Wright et al. (1973) examined unequal lowering or "telescoping" of various zones in the Chuska Mountains on the Arizona-New Mexico border. In recent years, the pendulum has swung to recognize that Pleistocene zonation is often without modern analog. Consequently, changes along the elevational gradient are now being scrutinized from the individualistic rather than Clemensian point of view. The individualistic approach has gained impetus in Southwestern paleoecology with the advent of packrat (*Neotoma* spp.) midden analysis, allowing great taxonomic and geographic precision for discerning past changes in the elevational range of individual plants. Along these lines, a major focus has been to reveal disharmonious plant associations in Wisconsin time (Cole 1981, Spaulding 1981).

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In high relief areas of western North America, steep gradients in plant zonation are often related to pronounced vertical variations in climate. Though no causal relationship has been demonstrated, it is assumed that mountain belts do in part explain the vertical distribution of plants. Quantitative estimates of past climates can be achieved by applying present gradients of precipitation and temperature to the amount of change in the elevational range of a plant. During the late Wisconsin, plants now limited to upper elevations expanded down to the surrounding lowlands. Prime examples include pinyon-juniper woodland in the Chihuahuan and Sonoran Deserts (Van Devender and Spaulding 1979) and depressions of up to 1000 m for Utah juniper (*Juniperus osteosperma*) and limber pine (*Pinus flexilis*) in the Mohave Desert (Spaulding 1981). Because rainfall increases and temperatures generally decrease with elevation, application of vertical gradients to characterize lowering of plant zones suggests both a cooler and wetter climate for the late Wisconsin of the western deserts.

Another way of deriving climate from the fossil plant record is suggested by the horizontal zonation of both plants and climate. During the late Wisconsin, the ranges of several plants expanded or contracted by several degrees in latitude. Notable examples are the southern expansion of Joshua tree (Yucca brevifolia) into the Sonoran Desert (Van Devender 1973) or the restriction of Colorado pinyon (*Pinus edulis*) to the northern Chihuahuan Desert (Van Devender et al., in press). These records are interesting because range boundaries often coincide with steep atmospheric gradients separating well-defined air masses. The northern and southern limits of the Canadian boreal forest coincide with the summer and winter position of the arctic front (Bryson 1966). Mitchell (1976) notes that of 73 tree species widely distributed in the western U.S., almost half reach their northern or southern limits between 40° and 44° N latitudes. North of this boundary, westerly flow from the Pacific Ocean predominates, but below the boundary flow is to the south, originating in an anticyclone over southern Nevada. Hypothetically, long-term displacement of this boundary would serve to either contract or expand the ranges of certain trees.

A critical area for tracing large-scale migration of plants relative to the development of modern plant zonation is encompassed in those portions of New Mexico, Arizona, Colorado and Utah collectively known as the Colorado Plateau Province (used here as the Colorado Plateaus). The vertical zonation of plants is relatively homogenous throughout the mountain ranges and higher plateaus that hover above the lower much-dissected tablelands. This homogeneity enhances the extrapolation of regional patterns from a few, strategic fossil localities. The area is also an excellent laboratory for studying the effects of shifting air flow patterns on regional vegetation. Mitchell's (1976) winter boundary coincides with the northern edge of the Colorado Plateaus, and the monsoonal boundary as defined by Bryson and Lowry (1955) crisscrosses the area from southwest to northeast. Both boundaries figure prominently in the biogeography of the western U.S.

To date, packrat midden data from the Colorado Plateaus include a Holocene chronology from Chaco Canyon, New Mexico (Betancourt and Van Devender 1981), late Pleistocene projections of lowland vegetation from the Chuska Mountain pollen sequence (Wright et al. 1973) compared with midden macrofossils from adjacent Canyon de Chelly, Arizona (Betancourt and Davis 1984), and gradient analysis of plant response to Pleistocene climates in the eastern Grand Canyon (Cole 1981, 1982). Until now, no fossil packrat middens had been collected from the central portion of the Colorado Plateaus in southeastern Utah.

The present study grew out of overall efforts to evaluate the feasibility of radioactive waste disposal in the Paradox Basin of Utah. Management and disposal require consideration of geologic and hydrologic processes expected to supervene during the toxic life of the waste (DeBuchananne 1974). Geohydrologic information is needed to predict potential transportation (by water) of radionuclides away from burial sites. One important parameter is the variability of past climate over relevant watersheds in time intervals comparable to the toxic life of the waste. Under contract with Woodward-Clyde Consultants of San Francisco, which was acting in behalf of the Office of Nuclear Waste Isolation, Battelle Memorial Institute, I undertook a midden study to reconstruct late Quaternary vegetation change, and, by inference, paleoclimatic variability for the central portion of the Colorado Plateaus.

The elevational gradient from the Abajo Mountains south along Comb Ridge to the San Juan River was chosen for geologic reasons. Large rock shelters containing middens of all ages are common in the local Navajo Sandstone (Glen Canyon Group; Jurassic). This sandstone outcrops continuously from 2560 to 1340 m as a consequence of deformation by the igneous intrusion that formed the Abajo Mountains. A brief reconnaissance of the 1220 m gradient produced two midden sequences from late Wisconsin times to the present in rock shelters at 1585 m and 2195 m elevation. Vertical gradients for both precipitation and temperature were derived from 18 climatic stations in southeastern Utah and are used to reconstruct climate at the fossil localities and elevational analogs for late Wisconsin plant assemblages. The midden record from southeastern Utah is also harnessed to generate new ideas about the historic development of vegetation patterns on the Colorado Plateaus.

METHODS

Packrat foraging for food and construction usually produces representative collections of the local flora. Because of predator pressure, packrats are tethered to within 100 m of their houses (Raun 1966, Bleich and Schwartz 1975, Stones and Hayward 1968). Seemingly amorphous piles of plant and other material seal passageways and interior chambers from predators and serve to buffer daily or seasonal extremes in temperatures. The outer crust of the houses and the floors of the passageways are often hard-packed with feces and crystallized urine (amberat). During times of high atmospheric humidity, the amberat rehydrates and permeates the lattice work of an abandoned house. This process combines with gradual collapse of the structure to create the indurate masses referred to as middens. Packrat feces, urine, and plant material dropped en route to the house may also produce middens in perch areas or trails along the walls of caves and rock shelters. Stratified deposits may form when packrats continue to build atop older middens. Problematical stratigraphy results when packrats build along the sides or even below older middens.

There is currently little agreement on field and laboratory procedures for packrat midden analysis. Generally, I collect middens with an indurated mass of 0.5 to 2.0 kg. Outer weathering surfaces are removed and the sample is carefully whittled down to the desired sample size with hammer and chisel. An individual sample is isolated that appears to represent a single depositional episode with a temporally discrete assemblage of plants. Samples are weighed prior to disaggregation in water (the amberat is water soluble), which may take from two to 10 days depending on the sample. The organic residue is wet-screened through a 20 mesh (0.84 mm) soil sieve to remove dust and urine still adhering to plant parts.

The organic residue caught by screening is weighed after drying in an oven and often comprises from 10 to 20 percent of the mass of the indurated midden. Initial sorting involves removal of all fecal pellets. The dry organic residue minus the fecal pellets yields the mass of plant matrix to be analyzed, which usually accounts for 50 to 70 percent of the dry weight of the washed sample. This plant matrix is sieved into size classes and hand sorted for identifiable fragments. On the average, individual middens yield from 20 to 30 kinds of plants.

Species representation is commonly expressed in terms of relative abundance, primarily because the original mass and number of unidentifiable fragments vary per kilogram of unwashed midden (Van Devender 1973, Phillips 1977, Spaulding 1981). A relative scale of one to five (1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant) is commonly used. Recently, other means of expressing macrofossil abundances have been suggested. Cole (1981) employs the concentration of macrofossils for each species per kilogram of indurated sample. The main pitfall in this strategy is the sample-to-sample variability in the concentration of amberat, sediment, rocks, and fecal pellets. Spaulding (in press) shows the relative frequency of a given taxon as a percentage of the total number of identified specimens, noting that often the numbers for a single taxon overwhelm the rest of the assemblage. This is avoided by subtracting the overrepresented taxon from the total number of identified specimens. Aside from the problem of comparing seeds and stems, this method is under the same constraints as pollen percentages (Davis 1963), whereby the percentage of one pollen or macrofossil type is mutually dependent on other types in the sample. To avoid these problems, I prefer to divide the mass of the species by that of the plant matrix in a midden, to include unidentified portions. This permits comparisons of the abundances for a single species throughout a lengthy midden sequence and between contemporaneous middens at various localities.

Radiocarbon dating of packrat middens has been the subject of much debate. Wells (1976) advocates dating mixed debris from a thin layer of midden. Van Devender (1973) and Mead et al. (1979) recommend dating either a single fragment (e.g., a piece of wood) or a composite sample from one species. The species targeted for dating should be critical to paleoecological reconstructions. For instance, in a midden study aimed at determining the arrival of pinyon (*Pinus edulis*) on the Colorado Plateaus, direct dates on pinyon macrofossils circumvent potential problems with mixed assemblages or questionable stratigraphy. When no species from a single midden yields sufficient material for a radiocarbon determination (greater than 3 g), a date on some other fraction such as packrat pellets may be necessary. Although the cost may be prohibitive, multiple dates on a single midden are often necessary. This becomes crucial where a single midden assemblage is employed as the keystone of a sequence, marking a biochronologic event or boundary. Multiple dates are also imperative in middens suspected of contamination. Spaulding (1981) reviews a series of middens with multiple dates, concluding that the dates were discordant at one standard deviation in 30 percent of the cases. However, in a number of the cases he examined, there was reason to doubt the first date based on questionable associations of plants in the assemblage. Confirmation of suspected contaminants, present only in trace amounts, will become routine with further development of accelerator dating.

Early midden research focused on the contrast between Wisconsin and modern vegetation. In the field, Wisconsin-age middens were easily recognized by the presence of plants now growing at much higher elevations or even different latitudes. For the user of midden data concerned with the historic continuum, the bias for Pleistocene middens produced many incomplete chronologies. The scant attention paid to younger middens partly reflected the sentiment that there had been little or no sequential change in Holocene vegetation. Recent midden studies in the Great Basin (Thompson and Hattori 1984), northern Chihuahuan Desert (Van Devender et al. in press) and the Colorado Plateaus (Betancourt and Van Devender 1981) demonstrate that Holocene migration of plants in the West may be as dynamic as postglacial invasion north of the glacial border. I would argue that much of this movement continues today. Moreover, historical explanation for present vegetation patterns can only be gleaned from chronologies that trace development of local vegetation over long periods of time. I prefer to hold the site constant for each chronology by developing lengthy midden sequences from individual rock shelters or caves. Hence, the floral composition for a plot of less than one hectare can be observed, even if sporadically, over thousands of years.

Physical Setting

The Colorado Plateaus are characterized by flat-lying sedimentary rocks, modified locally by faulting, folding, and igneous intrusions. The various "plateaus" are elevated from 1520 to 3350 m. Elevations below 1520 m are limited to the canyon bottoms of the Colorado River and its numerous tributaries. The central portion of the Plateaus is occupied by the spectacular Canyonlands of southeastern Utah. A tableland of resistant Dakota Sandstone, known locally as the Great Sage Plain but nonetheless much dissected, separates the La Sal and Abajo Mountains from the principal ranges of the southern Rocky Mountains. The Great Sage Plain is bordered on the west by the Monument Upwarp, boasting scenic buttes (monuments) and steep escarpments of Triassic and Jurassic sandstones. The crest of the upwarp is poorly defined at Elk Ridge, and the Comb Ridge monocline forms the steeply downfolded eastern edge. The latter is delineated by a comb-like crest of Navajo Sandstone stretching 160 km from west of Kayenta, Arizona, to the northeast base of Elk Ridge. The uplands in the area are defined by several laccolithic ranges, including the Ute, Henry, Navajo, La Sal, and Abajo mountains. At Navajo Mountain, the sedimentary rock has not eroded sufficiently to expose the igneous core, which outcrops at higher elevations in the other ranges. The higher peaks in the region are in the La Sal Mountains, rising up to 3877 m at Mount Peale (Gregory 1938). Only the La Sal Mountains were glaciated during the late Wisconsin interval (Richmond 1962, Witkind 1965).

Plant Zonation

Floristically, the La Sal and Abajo Mountains are considered outliers of the southern Rocky Mountains (Cronquist et al. 1972). There is also a close resemblance in the elevational range of plants. Below, I employ the zonal concept simply as an heuristic device without traditional ecological implications. In general, the upper elevational limits of each species occur on open, south-facing slopes, whereas the lower limits are usually defined on north-facing slopes or in mesic ravines. Alpine tundra is confined to the La Sal Mountains at elevations above 3660 m. Abajo Peak at 3660 m is the highest in the Abajo Mountains. From Mt. Linnaeus (3340 m) to the San Juan River (1340 m), plant zonation is as follows:

Engelmann spruce-alpine fir forest (3660-2896 m): Engelmann spruce (*Picea engelmannii*) and alpine fir (*Abies lasiocarpa*) are the dominant species of forests above 2896 m. Engelmann spruce is usually the more abundant as well as the taller of the two species in mixed stands. The herbaceous cover in closed stands is mostly depauperate due to the accumulation of duff and debris (Daubenmire 1943). Dense, spruce-fir stands are common mostly on steep, northerly exposures. Subalpine meadows cover extensive areas on the more gentle slopes. Common shrubs include currant (*Ribes* spp.), dwarf juniper (*Juniperus communis*), elderberry (*Sambucus racemosa*), blackberry (*Rubus idaeus*), snowberry (*Symphoricarpus oreophilus*), russet buffaloberry (*Shepherdia canadensis*), and boxleaf (*Pachystima myrsinites*). Limber pine (*Pinus flexilis*) is limited to dry, rocky exposures although it occasionally occurs within the spruce-fir forest. Aspen (*Populus tremuloides*) frequently occurs at the base of steep, south-facing exposures (Ellison 1954) and is most common in the lower part of the zone.

Douglas fir-white fir-blue spruce zone (3048-2438 m): The mixed conifer forest at these elevations is usually dominated by Douglas fir (*Pseudotsuga menziesii*), which has a broad elevational range. Douglas fir is distributed from the spruce-fir zone in the Abajo Mountains down to 1830 m in Natural Bridges National Monument. White fir (*Abies concolor*) and Douglas fir share dominance on sheltered and north-facing slopes. Riparian forests at these elevations are dominated by blue spruce, white fir, and aspen. Blue spruce often extends down to low elevations along the major canyon streams. Along upper Indian Creek on the north side of the Abajos, blue spruce can occur down to 2320 m. Xeric exposures in this zone are frequently occupied by limber pine at the higher elevations and ponderosa pine (*Pinus ponderosa*) on the lower slopes. Large portions of the exposed uplands may be clad in ponderosa pine forest at the lower elevations. Many of the understory shrubs in this mixed-conifer forest are the same as in the spruce-fir zone, with two important additions—Rocky Mountain maple (*Acer glabrum*) and serviceberry (*Amelanchier utahensis*).

Ponderosa pine-Gambel oak zone (2740-1830 m): This zone is dominated by ponderosa pine and the deciduous Gambel oak (*Quercus gambelii*). At higher elevations, extensive clones of Gambel oak apparently have developed from a single individual over a period of several hundred years. Ponderosa pine may form thick stands on the broken slopes of the Abajos, or occur as parkland as on Elk Ridge near Bear's Ears. Douglas fir commonly occurs in this zone, particularly at the base of cliffs with northerly exposures. Gallery forests with an overstory of ponderosa pine extend down to 1830 m in Cottonwood Wash and its tributaries. The lowest stand of ponderosa pine in the study area in a riparian setting is at 1700 m near the source of Butler Wash on the east side of Comb Ridge. The ponderosa pine–Gambel oak zone shares many shrubby species with the lower pinyon–juniper woodland. Some of the common trees and shrubs include Rocky Mountain juniper (*Juniperus scopulorum*), mountain mahogany (*Cercocarpus* spp.), serviceberry, snowberry, kinnick-kinnick (*Arctostaphylos uva-ursi*), buckbrush (*Ceanothus fendleri*), squawbush (*Rhus trilobata*), bitterbrush (*Purshia tridentata*), water birch (*Betula occidentalis*), rabbitbrush (*Chrysothamnus viscidifloris*), and big sagebrush (*Artemisia tridentata*).

Pinyon-juniper woodland and big sagebrush parkland (2290–1650 m): The dominant vegetation type in the area is a woodland of Colorado pinyon (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*). The area in pinyon-juniper woodland greatly exceeds that of the other vegetation zones; half of San Juan County lies between 1830 and 2130 m elevation. Pinyon may occur up to 9000 ft (2743 m), as on the summit of Bear's Ears on Elk Ridge. Scattered Utah junipers are not uncommon below 1520 m. In this zone, pure stands of big sagebrush often cover wide expanses, especially in the shallow divides at the heads of drainages and generally where soils are relatively deep but lack a well-developed calcic layer. Common shrubs in the pinyon-juniper woodland and sagebrush parkland include serviceberry, singleleaf ash (*Fraxinus anomala*), roundleaf buffaloberry (*Shepherdia rotundifolia*), mountain mahogany, rabbitbrush, snakeweed (*Gutierrezia* spp.), cliffrose (*Cowania mexicana*), Mormon tea (*Ephedra* spp.), yuccas (*Yucca* spp.), and prickly pear (*Opuntia polyacantha*).

Desert shrub zone (1650–1340 m): In the study area, this zone is more or less compressed due to the relatively high elevation of the San Juan River. Almost pure stands of blackbrush (*Coleogyne ramosissima*) occur on the sandy slopes west of Comb Wash, its upper limits overlapping the lower limits of Utah juniper. Typical stands in lower Road Canyon west of Comb Ridge are interspersed with galleta grass (*Hilaria jamesii*), Indian ricegrass (*Oryzopsis hymenoides*), snakeweed, and Mormon tea. Sand dunes in this zone are frequently vegetated by sand sagebrush (*Artemisia filifolia*), single-leaf ash, and sand oak (*Quercus undulata*). In the lower parts of the zone, shadscale (*Atriplex confertifolia*) is common though it seldom occurs in pure stands. Other common shrubs at these elevations include several saltbushes (*Atriplex* spp.), buckwheats (*Eriogonum* spp.), and greasewood (*Sarcobatus vermiculatus*). The latter is the principal phreatophyte in the zone and dominates the lower courses of Cottonwood, Butler, and Comb washes.

Climate

Probably the most useful scheme to describe air flow patterns over southeastern Utah is provided by Mitchell (1976), who uses equivalent potential temperature to determine seasonal locations of air mass boundaries over the western United States. Mitchell notes a winter pattern from November through March and a summer pattern from June through September, with April, May, and October as transitions between the two modes. Two equivalent potential temperature gradients, one in winter and the other in summer, traverse northern and southeastern Utah, respectively (Mitchell 1976, Fig. 3).

The winter gradient across northern Utah (ca 41° N lat.) coincides with a convergence zone. Flow below the boundary is southerly, originating in the anticyclone over southern Nevada. To the north, the flow is westerly from the Pacific Ocean. Several times during winter the anticyclone breaks down and allows storm tracks from the northern Pacific Ocean Aleutian Low to shift southward. This mechanism is responsible for most of the winter precipitation in southeastern Utah. The winter gradient separates cold, polar air from warmer subtropical air. The summer gradient, commonly called the monsoon boundary, runs diagonally from western Arizona, across southeastern Utah and northwestern Colorado, and into the Great Plains. During middle to late summer (July, August, and September), the area east of the boundary is under the influence of the Bermuda High over the Atlantic Ocean, but to the north, westerly flow from over the Pacific ocean predominates. Flow around the western end of the Bermuda High produces incursions of moist air over the southeastern part of the western United States. These incursions are responsible for the distinct summer rainy season over much of the Southwest. The subtropical moisture originates both from the Gulf of Mexico (Bryson and Lowry 1955) and from the Gulf of California (Hales 1974). Both the winter and summer gradients have been linked to jet stream patterns. The winter gradient has been related to the tropospheric polar jet stream (Reed 1979, Mullen 1979), whereas the monsoonal pattern is linked to the subtropical jet stream (Bryson and Lowry 1955).

Secular trends in the climate of the Southwest suggest that the two patterns, though occurring in different seasons, are in direct opposition throughout the year (Sellers 1960). This has broad implications for any consideration of past climates in southeastern Utah, particularly if trends of longer duration (on the order of several millennia) are caused by major shifts in the position of the jet streams. Generally, a southerly displacement of the polar jet stream produces a cooling trend; a warming trend is associated with a shift to the north. In the last 100 years, a warming trend occurred prior to 1940 and temperatures have been decreasing since that time in the northern hemisphere (Miles 1978). Nielson and Wullstein (1983) have examined the two trends as manifested in June and July latitudinal precipitation profiles along the gradient from Logan, Utah (42° N lat.) to Flagstaff, Arizona (35° N lat.). During the cooling trend, the monsoon withdraws to the south and its peak intensity shifts from July to August. Frequency patterns of early and late winter frontal systems occur approximately one month later than usual, significantly increasing June precipitation (late spring cyclonics from the north). June precipitation decreases from north to south along the gradient, opposite the trend for July. During warming trends, Nielson and Wullstein (1983) note an increase in July precipitation to the north, due to radial expansion of the Bermuda High. In Arizona, Sellers (1960) notes that September precipitation from a Pacific source is closely related to the precipitation for the preceding winter and that increases are favored by a southward displacement of the middle latitude storm track. Heavy September precipitation in Arizona is mostly related to tropical disturbances in the Pacific Ocean. The conditions favorable for high September precipitation are not favorable for July precipitation.

For southeastern Utah a southward displacement of the polar jet stream might result in increased winter precipitation, a decrease in midsummer precipitation, cooler summer temperatures, and a higher incidence of spring freezes. Possible increases in June and September precipitation may also be related to what Gifford et al. (1976) refer to as the Southern Utah Low. This is a high altitude low pressure system that today produces widespread precipitation in May and October, during the transition from winter cyclonic to summer anticyclonic circulation patterns. A northward shift of the jet stream (contraction of the polar vortex) might result in higher annual temperatures, a decrease in winter moisture, an increase in midsummer precipitation, and a relative dry late spring and foresummer.

As in other parts of the West, temperature and precipitation are greatly influenced by elevation in southeastern Utah. In general, air temperatures decrease and precipitation increases with elevation. In the Intermountain West, both relationships are largely linear for every month of the year (Price and Evans 1937, Baker 1944, Lull and Ellison 1950, Williams and Peck 1962, Houghton 1979). Vertical gradients for temperature and precipitation in winter (Oct.–Mar.), summer (Apr.–Sept.), and the hydrological year (Apr.–Sept.) were reconstructed from the last 20 years of record at 18 stations between 1209 and 2079 m in southeastern Utah (Table 1, Fig. 1). These gradients may be unusually low because the elevational range of the stations is small and they are all located in areas of relatively low relief below the base of the mountains. An annual rate of -0.59 C/100 m is recorded for the nearby San Juan Mountains of southwestern Colorado (Barry and Bradley 1976), a higher figure than the -0.45 C/100 m obtained for southeastern Utah. The regression equations for precipitation (Fig. 1) also grossly underestimate annual precipitation in the mountains. The Soil Conservation Service maintains two rain gauges near the lower limits for Engelmann spruce-alpine fir forest in the Abajo Mountains Camp Junction (2804 m) and Buckboard Flat (2865 m). Mean annual precipitation averaged over the past 20 years is 720 mm for Camp Junction and 790 mm at Buckboard Flat. The regression equations using data from lower elevations predict from 440 to 450 mm at these two sites, underestimating real precipitation by about 40 percent. The gradients for precipitation between Monticello (2079 m) and Buckboard Flat (2865 m) is ca 52 mm/100 m or 3 times steeper than the average rate calculated from the 18 stations below the base of the mountains. The steeper rate is comparable to the 41 mm/100 m

Table 1. Climatic stations and years of records used to calculate elevational gradients for temperature and precipitation in southeastern Utah.

Station	Elevation (m)	Latitude (North)	Longitude (West)	Temperature—years of record used	Precipitation—years of record used
Moab	1209	38°36'	109°36'	1962–1967, 1969–1971, 1973–1976, 1978–1979	1961–1980
Green River	1241	39°00'	110°10'	1961–1972, 1975	1961–1980
Dewey	1256	38°48'	109°18'	1970, 1973–1978, 1980	1968–1975, 1977–1980
Mexican Hat	1256	37°09'	109°52'	1961, 1963, 1966–1968, 1970–1971, 1973–1980	1961–1968, 1970–1980
Hanksville	1313	38°22'	110°43'	1961–1980	1961–1980
Bluff	1315	38°17'	109°33'	1962–1966, 1968–1980	1961–1980
Aneth Plant	1409	37°15'	109°20'	1966, 1968–1980	1966–1980
Hovenweep	1597	37°23'	109°05'	1961–1974, 1976–1980	1961–1980
Canyonlands—The Needle	1536	38°09'	109°45'	1966–1970, 1972, 1974, 1979–1980	1966–1980
Monument Valley Mission	1615	37°09'	110°13'	1964, 1966–1967, 1969–1970, 1972, 1974, 1979–1980	1963–1980
Capitol Reef Nat. Monument	1676	38°17'	111°16'	1968–1980	1968–1980
Castle Dale	1725	39°13'	111°01'	1961–1968, 1971–1980	1961–1980
Canyonlands—The Neck	1798	38°27'	109°50'	1966, 1968–1972, 1976–1980	1966–1980
Ferron	1807	39°05'	111°08'	1961–1969, 1971, 1973, 1976–1980	1961–1980
Blanding	1868	37°37'	109°28'	1961–1980	1961–1980
Natural Bridges	1981	37°37'	109°59'	1967, 1969–1977, 1979–1980	1966–1980
Cedar Point	2060	37°43'	109°05'	1964–1980	1961–1980
Monticello	2079	37°52'	109°18'	1961–1980	1961–1980

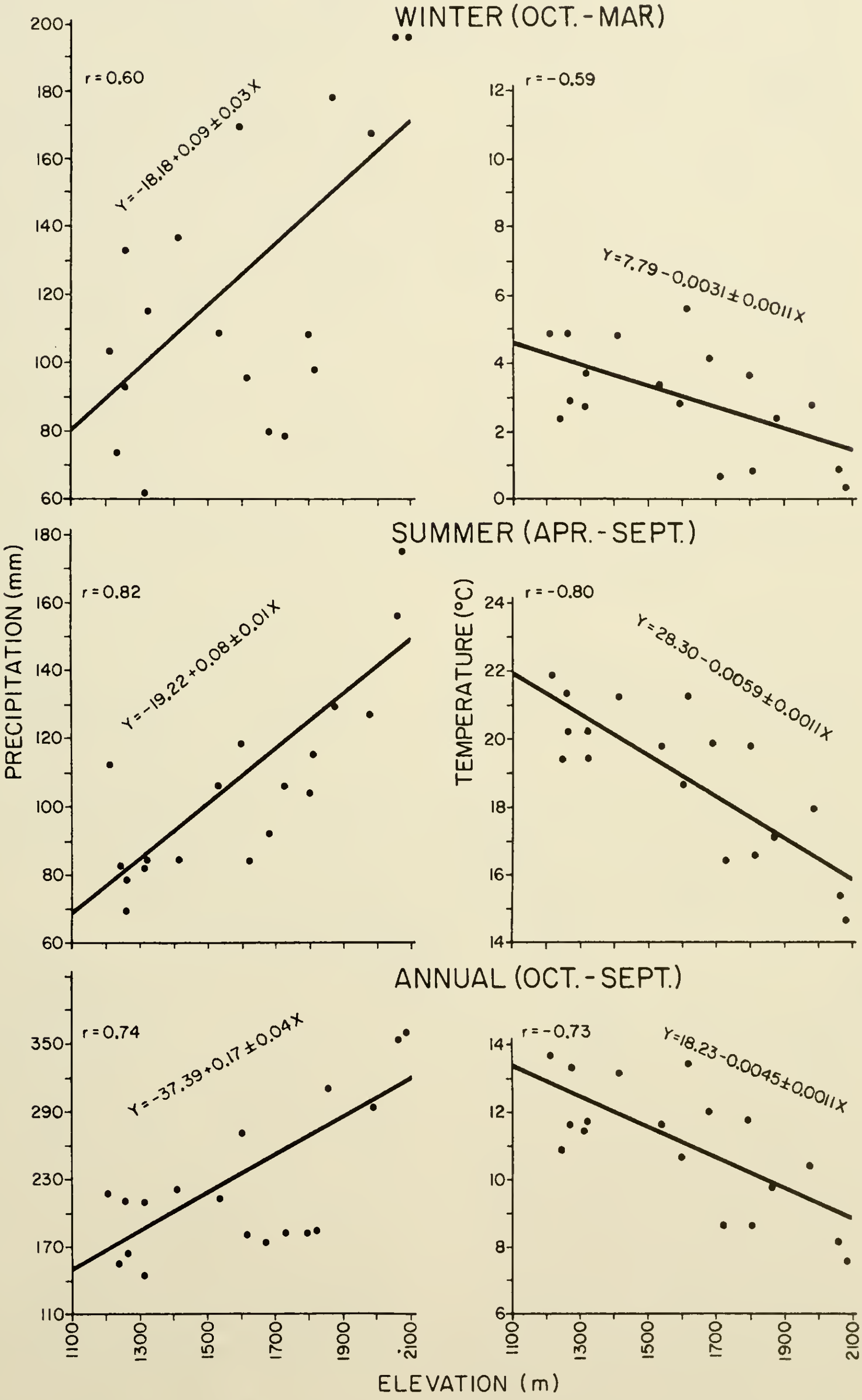

Fig. 1. Linear regressions that express the relationship between temperature and precipitation with elevation from 18 climatic stations in southeastern Utah.

cited for the Wasatch Plateau of central Utah, using data from an elevational range of 1690 to 3110 m (Lull and Ellison 1950).

Obviously, mountainous terrain has a greater physical effect on storm systems than the lesser plateaus. A significant difference lies in the steeper rates of increase for winter precipitation at higher elevations (above 2130 m). One explanation might involve seasonal variations in the type, areal extent, and direction of storm systems relative to the network of stations. In winter, convergent-type storms are subject to orographic uplift over a wide area. The paths of convective storms during summer are highly erratic, and the precipitation-elevation relationship is partly a function of a station's location along the path of an individual storm (Lull and Ellison 1950). An equally important factor is the temperature at the site of the precipitation. On cloudy days in winter, there may be no rainfall at the lower elevations, but snow is prevalent with the onset of freezing temperatures in the mountains.

The regression equations from Figure 1 are used later to predict climate at the elevations of fossil localities and the modern analogs for late Wisconsin assemblages. The lower rates associated with the 18 lowland stations should provide minimum estimates for the lower temperature and higher precipitation inferred for the last Wisconsin. The potential error in underestimating the steeper rates in mountainous terrain is taken into account.

RESULTS

Two large rock shelters along the Comb Ridge–Abajo Mountains gradient (Fig. 2) yielded midden sequences spanning the last 13,000 years. Fishmouth Cave (37°25'45"N, 109°39'W; 1585 m) is located on the east side of Comb Ridge, about 20 km northwest of Bluff. Allen Canyon Cave (37°47'30"N, 109°35'30"W; 2095 m) was spotted from the main road that skirts the base of Mt. Linneaus some 20 km northwest of Blanding.

Fishmouth Cave (Fig. 3) is a large shelter (75 m wide, 75 m deep, and up to 40 m high) that is plainly visible from several vantage points along the monoclinal valley of Butler Wash. The shelter has been visited by several notable geologists and archaeologists, but is mentioned only briefly in the literature. The inscription "Hyde Exploring Expedition, R. W., 1894" on the back wall refers to a visit from Richard Wetherill, an adventurous rancher financed by the expedition to reconnoiter prehistoric ruins in southeastern Utah. Prudden (1903:275) describes the cave briefly from Wetherill's correspondence. A photograph of the cave also appears in Gregory's (1938, Plate 23Ai) classic treatise on the geology of southeastern Utah.

Vegetation on slopes adjoining Fishmouth Cave can be described as juniper grassland. The lower edge of the pinyon-juniper woodland is but a few kilometers north along Comb Ridge and barely 50 m higher in elevation. Riparian vegetation along the deeply entrenched channel of Butler Wash is dominated by Fremont cottonwood (*Populus fremontii*), narrowleaf cottonwood (*Populus angustifolia*), and tamarisk (*Tamarix ramosissima*). Impenetrable thickets of young tamarisks choke the confluence of Butler Wash and the ravine leading out from the cave. Other common plants in the confluence area are willows (*Salix* spp.), greasewood (*Sarcobatus vermiculatus*), rabbitbrush (*Chrysothamnus nauseosus*), Russian thistle (*Salsola iberica*), fourwing saltbush (*Atriplex canescens*), and summer cypress (*Kochia* spp.). Table 2 lists plants found within 100 m of the cave entrance. Slope exposure near the cave entrance is to the northeast.

Allen Canyon Cave (Fig. 4) is a slightly smaller shelter located on the north side of a ridge of Navajo Sandstone separating Allen Canyon from an unnamed tributary in the area of Bayles Pasture. Both drainages have their sources on the west slopes of Mt. Linneaus, eventually flowing into South Cottonwood Wash, which closely parallels Butler Wash en route to the San Juan River. Mt. Linneaus (6.4 k distant) and the spruce-fir forest near its summit are neatly framed by the arched ceiling when one looks out from the cave. On the exposed ridge above the shelter, pinyon pine and Utah juniper predominate with scattered ponderosa pine. Along the base of the cliffs, the dominant tree is Douglas fir, with aspen groves located in pockets of deeper soils. On the gentle slope leading down to the level valley is a dense stand of Rocky Mountain maple (*Acer*

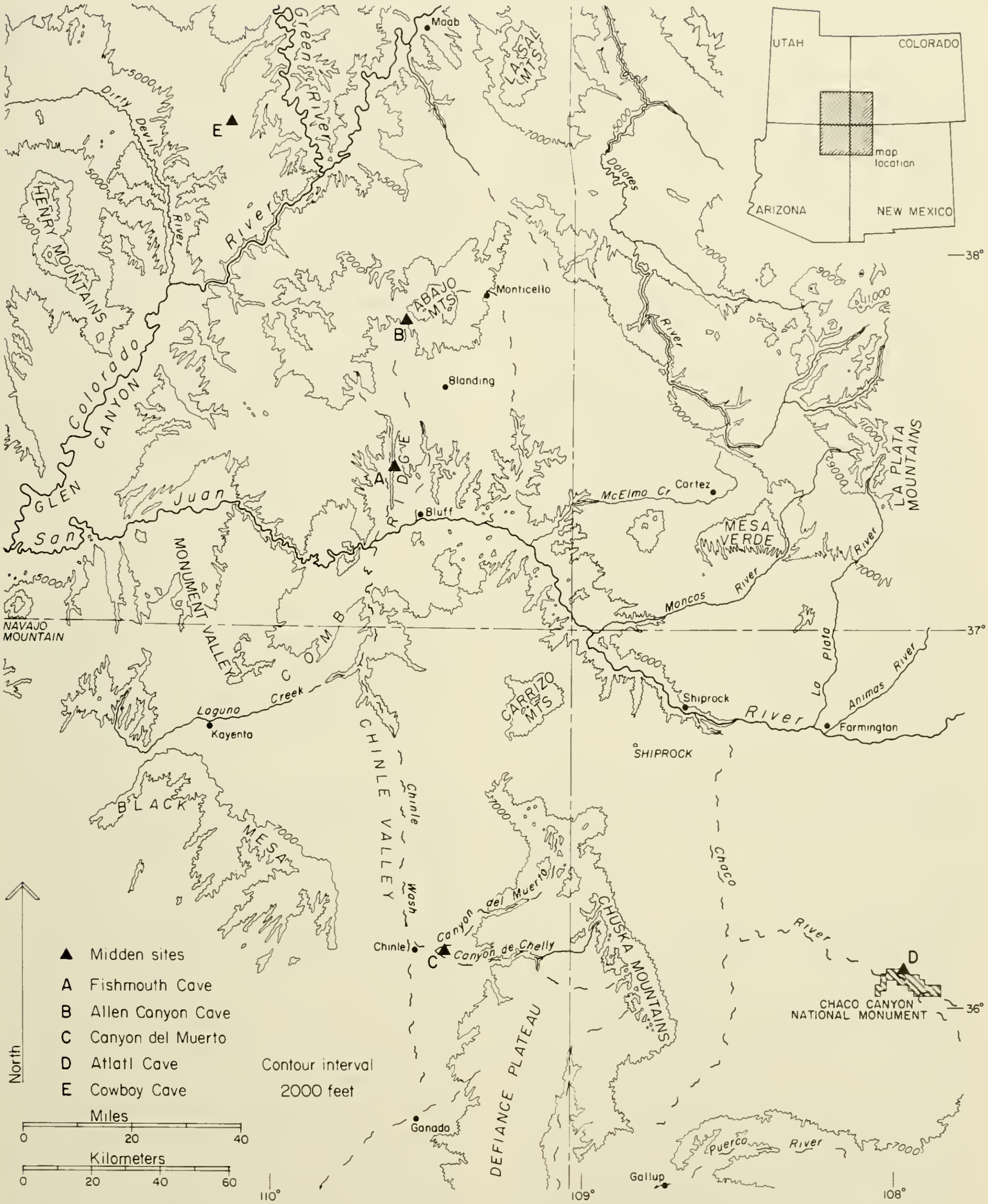
UTAH
COLORADO
ARIZONA
NEW MEXICO
map location
Moab
LA SAL MTS
Green River
Dirty Devil River
HENRY MOUNTAINS
E
Colorado River
GLEN CANYON
ABAJO MTS
B
Monticello
Blanding
Dolores River
A
COMB RIDGE
Bluff
San Juan
McElmo Cr
Cortez
MESA VERDE
LA PLATA MOUNTAINS
La Plata River
Mancos River
Animas River
Shiprock
River
Farmington
SHIPROCK
NAVAJO MOUNTAIN
MONUMENT VALLEY
COMB
Laguna Creek
Kayenta
CARRIZO MTS
CHINLE VALLEY
Chinle Wash
BLACK MESA
Canyon del Muerto
Canyon de Chelly
Chinle
C
CHUSKA MOUNTAINS
DEFIANCE PLATEAU
Chaco River
D
CHACO CANYON NATIONAL MONUMENT
Ganado
Gallup
Puerco River
5000
7000
9000
11,000
38°
37°
36°
110°
109°
108°
North
▲ Midden sites
A Fishmouth Cave
B Allen Canyon Cave
C Canyon del Muerto
D Atlatl Cave
E Cowboy Cave
Contour interval 2000 feet
Miles
0 20 40
Kilometers
0 20 40 60

Fig. 2. The central portion of the Colorado Plateaus showing location of fossil localities discussed in text.

glabrum), interspersed with Gambel oak, water birch (*Betula occidentalis*), and elderberry (*Sambucus* sp.). Table 3 lists plants growing on the northwest-facing slope in front of Allen Canyon Cave.

Eight middens (a total of 16) were collected from 40 to 50 middens scattered on the floor and talus of each cave. All middens were briefly inspected and samples were collected to represent the total variability in plant macrofossil assemblages. Based on field examination of midden surfaces and preliminary lists of plant macrofossils, I anticipated that both sequences encompassed the interval

Table 2. Plant list from within 100 m of Fishmouth Cave.

Agavaceae
Yucca angustissima Engelm. — narrowleaf yucca
Anacardiaceae
Rhus trilobata Nutt. — squawbush
Asclepiadaceae
Asclepias asperula (Decne.) Woodson — milkweed
Boraginaceae
Cryptantha jamesii (Torr.) Payson — catseye
Lappula redowskii (Hornem.) Greene — stickseed
Cactaceae
Opuntia phaeacantha Engelm. — variable prickly pear
Opuntia polyacantha Haw. — Plains prickly pear
Chenopodiaceae
Atriplex canescens (Pursh) Nutt. — fourwing saltbush
Ceratoides lanata (Pursh) J. T. Howell — winterfat
Cleomaceae
Cleome serrulata Pursh — Rocky Mountain beeweed
Compositae
Artemisia ludoviciana Nutt. — white sage
Artemisia tridentata Nutt. — big sagebrush
Aster sp. — aster
Brickellia californica (Torr. & Gray) Gray — brickellbush
Chrysothamnus nauseosus (Pall.) Britt. — rabbitbush
Gutierrezia sarothrae (Pursh) Britt. & Rusby — snakeweed
Heterotheca villosa (Pursh) Shinners — golden aster
Lygodesmia grandiflora (Nutt.) T. & G. — skeleton plant
Xanthium strumarium L. — cocklebur
Cruciferae
Stanleya pinnata (Pursh) Britton — desert plume
Cupressaceae
Juniperus osteosperma (Torr.) Little — Utah juniper
Elaegnaceae
Shepherdia rotundifolia Parry — roundleaf buffaloberry
Ephedraceae
Ephedra viridis Cov. — Mormon tea
Fagaceae
Quercus gambelii Nutt. — Gambel oak
Gramineae
Bouteloua barbata Lag. — sixweeks grama
Bouteloua curtipendula (Michx.) Torr. — sideoats grama
Bromus tectorum L. — cheatgrass
Hilaria jamesii (Torr.) Benth. — galleta
Oryzopsis hymenoides (Roem. & Schut.) Ricker — Indian ricegrass
Sitanion hystrix (Nutt.) J. G. Smith — bottlebrush
Juncaceae
Juncus sp. — rush
Leguminosae
Astragalus sp. — milkvetch
Melilotus albus Desr. — white sweet clover
Malvaceae
Sphaeralcea sp. — globemallow
Oleaceae
Fraxinus anomala Torr. — single leaf ash
Onagraceae
Oenothera hookeri T. & B. — evening primrose
Oenothera neomexicana (Small) Munz. — evening primrose
Polemoniaceae
Ipomopsis aggregata (Pursh) Spring. — shooting star
Polygonaceae
Eriogonum corymbosum Benth. — wild buckwheat
Eriogonum inflatum Torr. & Frem. — desert trumpet
Eriogonum alatum Torr. — winged buckwheat
Ranunculaceae
Clematis ligusticifolia Nutt. — virgin's bower
Rosaceae
Amelanchier utahensis Koehne — serviceberry
Cercocarpus intricatus S. Wats — littleleaf mountain mahogany
Salicaceae
Salix exigua Nutt. — coyote willow
Populus fremontii Wats. — Fremont cottonwood
Scrophulariaceae
Castilleja linariaefolia Benth. ex. DC. — Indian paintbrush
Cordylanthus wrightii Gray ex Torr. — birdbeak
Ulmaceae
Celtis reticulata Torr. — netleaf hackberry

from late Wisconsin to present. Table 4 lists the weight statistics for all middens, showing surprisingly little variation in the percentage of organic residue saved during washing or the concentration of fecal pellets per unit mass.

A total of 21 radiocarbon samples were used to determine the age of the 16 middens (Table 5). The material dated includes Douglas fir wood, needles, and buds, limber pine needles and seeds, Utah juniper twigs and seeds, and packrat pellets. At Fishmouth Cave, the midden sequence spans the interval from 12,770 to 2260 B.P. The Allen Canyon series encompasses the period from 11,310 to 1820 B.P. At both localities the oldest samples (greater than 9000 B.P.) were all found on the steep talus toward the front of the shelter. Younger middens are most common on roof fall and ledges deeper inside the shelter. This pattern is partly the result of natural exfoliation from the interior walls. As the back walls recede, old roof falls are buried by progressively younger ones. Outcrops of the oldest roof falls occur toward the front of the shelter. If a threshold slope has been reached on the steep talus, the downslope waste of the younger material may continue to expose the outcrop of older roof fall. The high incidence of rock slides may discourage packrats from occupying the front talus, forcing

Table 3. Plant list from within 100 m of Allen Canyon Cave.

Aceraceae
Acer glabrum Torr. — Rocky Mountain maple
Agavaceae
Yucca angustissima Engelm. — narrow leaf yucca
Anacardiaceae
Rhus radicans L. var. *rydbergii* (Small) — poison ivy
Rhus trilobata Nutt. — squawbush
Betulaceae
Betula occidentalis Hook. — water birch
Boraginaceae
Cryptantha sp. — catseye
Hackelia pinetorum (Greene) Johnst. — stickseed
Cactaceae
Opuntia polyacantha Haw. — Plains prickly pear
Caprifoliaceae
Sambucus sp. — elderberry
Celestraceae
Pachystima myrsinites (Pursh) Raf. — mountain lover
Chenopodiaceae
Chenopodium sp. — goosefoot
Compositae
Antennaria sp. — pussytoes
Artemisia ludoviciana Nutt. — white sage
Aster sp. — aster
Brickellia grandiflora (Hook.) Nutt. — large-flowered thoroughwort
Chrysothamnus viscidiflorus (Hook.) Nutt. — rabbitbrush
Solidago missouriensis Nutt. — goldenrod
Tragopogon dubius — goatsbeard
Cruciferae
Stanleya pinnata (Pursh) Britton — desert plume
Cupressaceae
Juniperus osteosperma (Torr.) Little — Utah juniper
Juniperus scopulorum Sarg. — Rocky Mountain juniper
Ericaceae
Arctostaphylos uva-ursi (L.) Spreng. — kinnick-kinnick
Fagaceae
Quercus gambelii Nutt. — Gambel oak
Gramineae
Festuca sp. — fescue
Muhlenbergia sp. — muhly
Hydrophyllaceae
Phacelia sp. — phacelia
Hypnaceae
Hypnum cupressiforme Hedw. — moss
Leskeaceae
Thuidium abietinum (Brid.) BSG — moss
Liliaceae
Allium sp. — wild onion
Onagraceae
Oenothera neomexicana (Small) Munz — evening primrose
Pinaceae
Pinus edulis Engelm. — Colorado pinyon
Pinus ponderosa var. *scopulorum* Engelm. — ponderosa pine
Pseudotsuga menziesii (Mirb.) Franco — Douglas fir
Polemoniaceae
Ipomopsis aggregata (Pursh) Spengl. — skyrocket

Table 3 continued.

Polypodiaceae
Cheilanthes sp. — lipfern
Rosaceae
Amelanchier utahensis Koehne — Utah serviceberry
Cercocarpus intricatus Wats. — little leaf mountain mahogany
Holodiscus dumosa (Nutt.) Heller — shrubby creambush
Prunus virginiana L. — western chokecherry
Rubus sp. — blackberry
Salicaceae
Populus tremuloides Michx. — aspen
Saxifragaceae
Ribes aureum Pursh. — golden currant

them to gentler grades toward the back and sides of the shelter.

Cole and Mayer (1982) discuss a similar pattern for caves in the Redwall Limestone of the eastern Grand Canyon, where the oldest middens are preserved nearest the cave entrances. Their model involves rapid retreat of the cliff face, rather than exfoliation of the interior walls, as influencing the age and spatial distribution of middens. The effect of roof falls as a burying agent may not apply in the relatively narrow caves of the Redwall Limestone. Increasing darkness with depth may be a deterrent to packrat activity beyond the entrance area in the Grand Canyon caves, so that midden preservation is affected mostly by cliff retreat and not by roof collapse.

Multiple dates were used to test the temporal integrity of four of the midden assemblages. The rationale for redating these assemblages is as follows.

FC 2 is the only loose, unindurated midden collected from either of the two localities. Because the macrofossils from FC 2 were not encased in hardened urine since the time of deposition, at least low levels of contamination were anticipated. Initial sorting of the midden revealed no anomalies. Nonetheless, we independently dated Douglas fir needles (9340 B.P.) and packrat fecal pellets (10,360 B.P.). These dates are within the 1000 year uncertainty recommended by Klein et al. (1982) to account for cosmic ray flux in samples older than 8000 B. P. Based on the lack of Utah juniper in this sample, which first appears in FC 5 at 9700 B.P., FC 2 is assigned the older date of 10,360 + 80 B.P.

FC 3 is an indurated midden which contains a mix of Utah and Rocky Mountain juniper associated with limber pine and Douglas fir. No other middens from this locality record these junipers. Older assemblages only have Rocky Mountain juniper, and samples younger than 9700 B.P. contain Utah juniper, which is at the site today and is the most likely candidate for contamination in older middens. While it is conceivable that FC 3 represents a time when both junipers grew at the site, independent dates on Douglas fir (10,540 ± 180 B.P.) and on Utah juniper (2790 ± 100 B.P.) failed to bear this out. Because of the great discrepancy between the two dates, this sample was excluded from further analysis.

AC 1 is an early Holocene assemblage, where I suspected no contamination but wished to test potential differences between dates from a single wood fragment and a composite sample of specimens from the same species, in this case Douglas fir. The two dates overlap at two standard deviations. An equal portion of the same Douglas fir branch was dated by a second C-14 facility with comparable results.

Redating of AC 8 was the most problematical. An initial date of 7350 ± 100 B.P. suggests that limber pine, spruce, and other montane elements persisted until the middle Holocene. Another midden (AC 2) nearby lacks these elements and records the arrival of several new taxa at 7200 ± 90 B.P. Two lines of reasoning suggest that the 7530 B.P. date is incorrect. Primarily, AC 8 is similar in macrofossil composition to AC 1 and AC 9, which dated at ca 10,000 B.P. Also, the difference in assemblages between AC 8 and AC 2 is so great, yet the age differences so negligible, that these middens either mark an abrupt vegetation change or one or both of the dates are incorrect. I chose to redate AC 8, anticipating a new date of ca 10,000 B.P. I accept the second date of 10,140 ± 190 B.P. and reject the first date of 7530 ± 200 B.P.

TABLE 4. Weight statistics of middens from Fishmouth Cave (FC) and Allen Canyon Cave (AC). All weights in grams.

Midden number	Indurated weight (i)	Washed weight (w)	w/i (%)	Neotoma pellets (p)	p/w (%)	Plant matrix (w-p)
FC 1	993.6	162.5	16.35	75.6	46.52	86.9
FC 2*	-	178.0	-	163.3	58.74	114.7
FC 3	1312.6	236.8	18.04	112.4	47.47	124.4
FC 4	842.1	123.6	14.68	54.4	44.01	69.2
FC 5	842.1	182.9	21.72	70.2	38.38	112.7
FC 6	1181.2	201.6	17.07	51.4	25.50	150.2
FC 7	1125.8	247.0	21.94	103.1	41.74	143.9
FC 9	879.8	108.7	12.36	46.4	42.69	62.3
MEAN	1025.3	192.6	17.45	84.6	43.13	108.0
AC 1	916.1	166.6	18.19	72.5	43.51	94.1
AC 2	868.0	114.2	13.16	54.7	47.90	59.5
AC 4**	1951.7	98.7	5.06	32.4	34.58	66.3
AC 5	1105.6	110.6	10.00	39.7	35.90	70.9
AC 6	952.1	69.4	7.29	25.6	36.89	43.8
AC 7	1724.8	175.3	10.16	54.3	30.97	121.0
AC 8	1178.9	181.6	15.40	82.0	45.15	99.6
AC 9	1081.1	128.4	11.88	55.6	43.30	72.8
MEAN	1222.1	130.6	11.39	52.1	39.78	78.5

*Loose, unindurated deposit collected in niche created by boulders on talus slope.

**Uriniferous sample collected directly below ledge where modern packrats continue to perch today. Crystallized urine was denser than in the other samples from this locality.

To accept the latter would require explaining a 2,000-year lag time between similar vegetation changes at Fishmouth Cave and the Allen Canyon locality.

At both rockshelters, low levels of contamination were anticipated because middens spanning several millennia occur side by side across the large floor areas. Unindurated middens of considerable age (e.g., FC 2) provide loose plant material for construction of much younger houses. For this reason, traces of Douglas fir (1 or 2 needles) are likely contaminants in FC 6 and FC 9. The same might be true for the single limber pine needle in FC 4. At the Allen Canyon locality, a single limber pine needle was in AC 2 and is considered anomalous to the rest of the assemblage. A single Utah juniper twig in AC 9 may represent a younger contaminant.

Seven middens from Fishmouth Cave yielded a total of 67 taxa, with an average of 21 taxa per sample (Table 6). At the Allen Canyon locality, 73 taxa were identified from eight middens, with a mean of 25 taxa per sample (Table 7). The number of taxa per midden does not appear to be a function of sample size, at least not in a positive sense. The Spearman rank-difference correlation coefficient was computed for the paired observations of number of taxa and the mass of the plant matrix. Surprisingly, a high negative correlation (rho = –0.652) was obtained. Table 8 shows that the negative correlation arises from my inherent bias to collect larger samples from middens with extralocal plants combined with a tendency for the oldest samples to yield low numbers of taxa. In the time series for the Allen Canyon locality, a strong trend emerges when the ratios for number of taxa to mass of the plant matrix are compared (Table 8). In the four oldest samples (late Pleistocene–early Holocene), this ratio ranges from 0.17 to 0.32. In the youngest four samples (middle to late Holocene), the values range from 0.38 to 0.62. This trend is not apparent at Fishmouth Cave.

TABLE 5. Radiocarbon dates on packrat middens from Fishmouth (FC) and Allen Canyon (AC) caves, San Juan County, Utah. All dates are calculated on the Libby half-life of 5568 years.

Midden	Age	Laboratory number	Material dated
FC 1	12,770 ± 140	BETA-5582	*Pinus flexilis* needles and seeds
FC 2	10,360 ± 80	BETA-5761	*Neotoma* fecal pellets
FC 2	9,340 ± 290	BETA-5762	*Pseudotsuga menziesii* needles, twigs, and buds
FE 3	10,540 ± 180	BETA-5757	*Pseudotsuga menziesii* needles, twigs, and buds
FC 3	2,790 ± 100	BETA-5758	*Juniperus osteosperma* twigs and seeds
FC 5	9,700 ± 110	BETA-5763	*Juniperus osteosperma* twigs and seeds
FC 4	6,100 ± 100	BETA-5759	*Juniperus osteosperma* twigs and seeds
FC 7	3,740 ± 70	BETA-5584	*Juniperus osteosperma* twigs and seeds
FC 6	3,550 ± 60	BETA-5764	*Juniperus osteosperma* twigs and seeds
FC 9	2,260 ± 90	BETA-5765	*Juniperus osteosperma* twigs and seeds
AC 7	11,310 ± 200	BETA-5756	*Pinus flexilis* needles
AC 9	10,070 ± 70	BETA-5767	*Neotoma fecal* pellets
AC 1	10,030 ± 330	BETA-5760	*Pseudotsuga menziesii* needles, twigs, and buds
AC 1	9,660 ± 140	BETA-5589	*P. menziesii* wood
AC 1	10,030 ± 200	DIC-2598	*P. menziesii* (same branch as BETA-5589)
AC 8	10,140 ± 190	A-3120	*Neotoma fecal* pellets
AC 8	7,530 ± 200	BETA-5588	*Pseudotsuga menziesii* needles, twigs, and buds
AC 2	7,200 ± 90	BETA-5586	*Neotoma fecal* pellets
AC 6	3,400 ± 60	BETA-5583	*Neotoma fecal* pellets
AC 5	3,000 ± 70	BETA-5585	*Neotoma fecal* pellets
AC 4	1,820 ± 50	BETA-5766	*Neotoma fecal* pellets

TABLE 6. Plant macrofossils and their relative abundances in fossil packrat middens from Fishmouth Cave, San Juan County, Utah. 1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant, ? = possible contaminant.

Species	Common name	12,770 ± 140 FC 1	10,360 ± 80 9380 ± 290 FC 2	9700 ± 110 FC 5	6100 ± 100 FC 4	3740 ± 70 FC 7	3350 ± 60 FC 6	2260 ± 90 FC 9
TREES, SHRUBS, AND SUCCULENTS								
cf *Alnus*	alder			2				
Amelanchier utahensis	Utah serviceberry		4	2	2	2	2	2
Artemisia tridentata-type	sagebrush			3			2	
Atriplex canescens	fourwing saltbush			2	2		2	2
Atriplex sp. (not *A. canescens*)								3
Ceanothus cf *fendleri*	buckbrush					1		
Celtis reticulata	netleaf hackberry			2				
Ceratoides lanata	winterfat				2		2	
Cercocarpus intricatus	littleleaf mountain mahogany			3	3	2	2	2
Cercocarpus montanus	alderleaf mountain mahogany	2	2					
Chrysothamnus sp.	rabbitbush	2						
Cornus stolonifera	red osier dogwood	4	1	1				
Coryphantha sp.								1
Cowania mexicana	cliffrose							3
Ephedra viridis	Mormon tea				3			
Ephedra sp.	Mormon tea	2		2		3	3	3
Fraxinus anomala	singleleaf ash						2	1
Gutierrezia sarothrae	snakeweed			1		1	2	3
Juniperus communis	common juniper	3						
Juniperus osteosperma	Utah juniper			5	5	5	5	5
Juniperus scopulorum	Rocky Mountain juniper	4	3					
Opuntia polyacantha	plains prickly pear	2	3	3	3	2	2	3
Picea pungens	blue spruce	2						
Pinus edulis	Colorado pinyon					3		
Pinus flexilis	limber pine	5	3		1?			
Pseudotsuga menziesii	Douglas fir	5	5	3	3		1?	1?
Prunus sp.	chokecherry		1					
Purshia tridentata	bitterbrush							1
Quercus gambelii	Gambel oak		4	2	2			
Rhus trilobata	squawbush		2	1	3	2	3	2
Rosa woodsii	rose	2						
Shepherdia rotundifolia	buffaloberry							1
Sclerocactus sp.	sclerocactus				1			
Yucca angustissima	narrowleaf yucca	1		3	1	2	2	
HERBS								
Artemisia ludoviciana	white sage	1	2	2				2
Astragalus	milkvetch	1						
Brickellia sp.	brickellbush				1			2
Chenopodium sp.	goosefoot		2					
Cirsium sp.	thistle	2						
Cryptantha sp.	catseye					1		2
Euphorbia sp.	spurge				1		1	
Helianthus sp.	sunflower	2		2	2			2
Heterotheca villosa	golden aster					2		
cf *Hymenoxys*	hymenoxys							1
cf *Ipomopsis*	gilia	1		1				1
Lappula redowskii	stickseed	1						1
Lepidium sp.	peppergrass				1			2

Table 6 continued.

Species	Common name	12,770 ± 140 FC 1	10,360 ± 80 9380 ± 290 FC 2	9700 ± 110 FC 5	6100 ± 100 FC 4	3740 ± 70 FC 7	3350 ± 60 FC 6	2260 ± 90 FC 9
Plantago sp.	Indian plantain			1				
Polygonum sp.	knotweed	1						
Sphaeralcea sp.	globemallow		1					
Thuidium abietinum	moss					1		
GRASSES								
Agropyron sp.	wheatgrass			1				
Agropyron cf *smithii*	wheatgrass							1
Andropogon scoparius	little bluestem					1		
Bouteloua barbata	sixweeks grama				1		1	
Bouteloua curtipendula	sideoats grama			1				1
Echinochloa crusgallii	barnyard grass				1			
Enneapogon desvauxii	spike pappusgrass						1	
Festuca ovina	fescue			1			1	1
Hilaria jamesii	galleta				1	1		
Hordeum cf *pusillum*	little barley							1
Koeleria cristata	crested wheatgrass							1
Muhlenbergia cf *pungens*	pungent muhly						1	
Munroa squarrosa	false buffalograss							1
Oryzopsis hymenoides	Indian ricegrass	2			4	3	3	1
Poa cf *fendleriana*	muttongrass			2			2	1
Number of taxa (N) = 67		N = 20	N = 13	N = 24	N = 20	N = 16	N = 20	N = 32

At Allen Canyon one is tempted to infer an increase for species diversity in the plant community during the middle and late Holocene. Species diversity in modern subalpine communities (late Pleistocene and early Holocene assemblages) is generally lower than for pinyon-juniper woodland or stands of Douglas fir–ponderosa pine (middle and late Holocene assemblages). This observation is substantiated for modern vegetation on the northern Colorado Front Range (Peet 1978, Figs. 1 and 4). Other explanations might be equally viable and would only demonstrate the difficulty in interpreting the number of taxa identified from packrat middens. Particularly relevant is the notion that the number of taxa is also a function of my own ability to identify plant parts. Greater familiarity with understory plants in pinyon-juniper woodland than in subalpine forest might produce a pattern similar to that noted for the Allen Canyon sequence.

A total of 106 plant taxa was identified from the 15 middens reported in Tables 6 and 7. Of these, 34 are shared by both the Fishmouth Cave and Allen Canyon sequences. In the majority of cases positive identification was accomplished by matching the macrofossil to modern voucher specimens at the Laboratory of Paleoenvironmental Studies and the Herbarium, University of Arizona. I was unable to identify a number of macrofossils from each midden. Some of these are distinctive and may be identified in the course of future work.

Separations within a few genera require further explanation. Blue spruce (*Picea pungens*) and Engelmann spruce (*P. engelmannii*) can be separated on the internal anatomy of the needles. Needles from each midden were immersed in water for about 1 week to soften. Thin sections were prepared, mounted on slides, and viewed through a compound microscope at various magnifications. All spruce needles from the two sequences can be relegated to either blue or Engelmann spruce. They are separated from other coniferous species by the four-angled or square cross sections of the needles, and the presence and position of the resin ducts (Durrell

TABLE 7. Plant macrofossils and their relative abundances in fossil packrat middens from Allen Canyon Cave, San Juan County, Utah. 1 = rare, 2 = uncommon, 3 = common, 4 = very common, 5 = abundant, ? = possible contaminant.

		11,310 ± 200	10,140 ± 190	10,070 ± 70	10,030 ± 200 10,030 ± 330 9660 ± 140	7200 ± 90	3400 ± 60	3000 ± 70	1820 ± 50
Species	Common name	AC 7	AC 8	AC 9	AC 1	AC 2	AC 6	AC 5	AC 4
TREES, SHRUBS AND SUCCULENTS									
Abies lasiocarpa	subalpine fir	4	1		2				
Acer glabrum	Rocky Mountain maple	2	2	1	2	1			
Amelanchier utahensis	Utah serviceberry	1	2	1		2	2	2	2
Arctostaphylos cf. *uva-ursi*	kinnick-kinnick			1			2	2	2
Cercocarpus montanus	alderleaf mountain mahogany								1
Cercocarpus intricatus	littleleaf mountain mahogany				1	2	2	2	3
Cornus stolonifera	red osier dogwood	2	2	2	2	2	1		2
Coryphantha sp.	coryphantha			3					
Gutierrezia sarothrae	snakeweed						1		
Juniperus communis	common juniper	4	2		3	3	2		
Juniperus osteosperma	Utah juniper				1?	2	3	3	2
Juniperus scopulorum	Rocky Mountain juniper					2	1	2	
Opuntia polyacantha	Plains prickly pear						1	3	3
Pachystima myrsinites	boxleaf	2	2	3	2	2	2	3	
Picea engelmannii	Englemann spruce	5		2					
Picea pungens	blue spruce		2		2				
Pinus edulis	Colorado pinyon						5	5	4
Pinus flexilis	limber pine	5	4	3	4	1?			
Pinus ponderosa	ponderosa pine		1	2	1	5	2	2	2
Prunus sp.	chokecherry							1	
Pseudotsuga menziesii	Douglas fir	2	5	5	5	4	4	4	4
Purshia tridentata	bitterbrush			1				2	
Quercus gambelii	Gambel oak		1			2	1	2	1
Rhus radicans	poison ivy					1		1	
Rhus trilobata	squawbush					2	2	2	
Rosa sp.	rose			1		1			
Rosa woodsii	rose	2	2		2				
Rosa cf. *nutkana*	rose			1					
Rubus sp.	blackberry	3	2	2	2	2		1	
Sambucus racemosa	elderberry	2		2	1				
Shepherdia canadensis	russet buffaloberry	3	3	3	3				
Yucca angustissima	narrowleaf yucca						2	1	1
HERBS AND MOSSES									
Amaranthus sp.	pigweed							1	1
Antennaria sp.	pussytoes					2			
Artemisia frigida	estafiata							2	
Artemisia ludoviciana	Mexican sage						1	2	
Aster sp.	aster		1	1					1
Centaurea sp.	starthistle					3			
Cirsium sp.	thistle			1					
Clematis sp.	virgin's bower					1			
Cryptantha sp.	catseye					1	2	1	
Eriogonum sp.	wild buckwheat					1			
Equisetum hyemale	scouring rush				1				
cf. *Helenium*	sneezeweed								1
Helianthus sp.	sunflower						1	1	
Heterotheca sp.	golden aster	2	1	1		1	2	1	1
Hypnum cupressiforme	moss	1	1			1		1	
Lithospermum sp.	stoneseed					1	1		2
Lupinus sp.	lupine						2		

Table 7 continued.

Species	Common name	11,310 ± 200 AC 7	10,140 ± 190 AC 8	10,070 ± 70 AC 9	10,030 ± 200 10,030 ± 330 9660 ± 140 AC 1	7200 ± 90 AC 2	3400 ± 60 AC 6	3000 ± 70 AC 5	1820 ± 50 AC 4
Physalis sp.	groundcherry								2
Polygonum sp.	knotweed	2	2	1				1	1
Potentilla sp.	cinquefoil	1							
Ranunculus sp.	buttercup					2	2		2
Selaginella sp.	selaginella						1	1	
Thalictrum fendleri	meadowrue	2	1						
Thuidium abietinum	moss	1					1	1	
GRASSES									
Agropyron sp.	wheatgrass							1	1
Agropyron cf. *smithii*	wheatgrass	1							
Brachiaria arizonicum	brachiaria					1			
Bromus anomalus	nodding brome	1	1						
Bouteloua gracilis	blue grama			1		1			
Deschampsia caespitosa	tufted hairgrass	1		2					
Festuca ovina	sheep fescue	1							
Hilaria jamesii	galleta						1		
Koeleria cristata	crested wheatgrass	2						2	1
Muhlenbergia sp.	muhly			1					
Muhlenbergia arsenei	muhly							1	
Oryzopsis hymenoides	Indian ricegrass						1	2	2
Panicum sp.	panic grass			1		1			
Poa cf. *fendleriana*	muttongrass	2	1			3	1	2	2
Sitanion-type	squirreltail					1			
Stipa comata	needle and thread grass								1
Trisetum spicatum	spike trisetum	1							
Number of taxa (N) = 73		26	22	23	16	30	27	33	25

1916). The two species were further distinguished on the relative size and position of the resin ducts. Blue spruce has relatively small resin ducts (less than one-fourth the size of the vascular bundle) touching the epidermis at the lateral angles. Engelmann spruce has large resin canals (greater than half and up to three-fourths the size of the vascular bundle) touching the epidermis at the sides. The distinction is important in comparing Fishmouth Cave (blue spruce only) with Allen Canyon (both), or the late Pleistocene (Engelmann spruce only) to the early Holocene (both) at Allen Canyon.

Three species of junipers (*Juniperus communis, J. scopulorum*, and *J. osteosperma*) are present in both midden sequences. Common juniper, a circumpolar species that occurs in subalpine forests of the Abajo and La Sal mountains, is the easiest to identify. The most common macrofossils are the broad, needlelike leaves or scales, often twisted so that the dorsal surface bears a white band of stomata. Scalelike leaves of Rocky Mountain juniper and Utah juniper are separated on the presence of minute teeth along the scale margins in Utah juniper and the presence of an elliptic resin gland on the dorsal surface of Rocky Mountain juniper scales. The gland in Utah juniper scales is deeply embedded in the mesophyll and is seldom visible on the surface (Vasek 1966). Some difficulty may arise in distinguishing Utah juniper from its close relative, one-seed juniper (*J. monosperma*), which also has denticulate margins on the scales. However, the resin gland is often visible in one-seed juniper scales.

Fir (*Abies*) is represented in the Allen Canyon sequence by alpine fir. Alpine fir can be distinguished from white fir on the basis of external morphology of the needles. Alpine fir has relatively short needles (less than 3 cm) with a retuse or notched tip, and white fir has longer needles (greater than 3 cm) with rounded to acute tips. Although it was not necessary to cross-section the needles, the position of the resin ducts may be the most reliable way to tell the two species apart. In white fir, the resin ducts are external (located contiguous to the epidermis), but in alpine fir they occur in the area of the mesophyll away from the epidermis (Durrell 1916).

The needles of ponderosa and limber pine were identified on the basis of external morphology. The strong serrations on needles originating from fascicles of three are diagnostic of ponderosa pine. AC 1, AC 9 and AC 2 produced strongly serrated needles from fascicles of two that could be referrable to lodgepole (*P. contorta*) or ponderosa pine on the basis of external morphology (W. B. Critchfield, pers. comm.). However, in all three samples these specimens are clearly outnumbered by needles from fascicles of three. The Rocky Mountain race of ponderosa pine (*P. ponderosa* var. *scopulorum*) occasionally produces fascicles of two, whereas fascicles of three in lodgepole pine are known only at its northernmost stations in the Yukon (Critchfield 1980). We thus refer all the strongly serrated needles in the middens to ponderosa pine.

Needles lacking strong serrations on the margins and originating from fascicles of five are identified as limber pine. They are distinguished from the bristlecone pines (*P. longaeva* and *P. aristata*) by having both dorsal and ventral stomata (bristlecone pine needles lack dorsal stomata) and needle length (less than 4 cm for bristlecone and from 4 to 10 cm for limber pine) (Harlow 1931). There is greater difficulty in separating needles of limber pine from its close relative, southwestern white pine (*P. strobiformis*). Southwestern white pine has discernible serrations (but weak, compared to ponderosa pine) and dorsal stomata limited to one or a few partial rows. Limber pine lacks serrations, or they are minute and sparse, and two or more rows of stomata are present on the dorsal surface of the needles (Steinhoff and Andersen 1971). A few of the needles in the Allen Canyon series resemble Southwestern white pine, yet the nearest stands are in the Sangre de Cristo Mountains of northern New Mexico and the White Mountains of east central Arizona. All

Table 8. Comparisons of number of taxa (N) to plant matrix (w-p) in fossil packrat middens from Fishmouth Cave (FC) and Allen Canyon Cave (AC), southeastern Utah.

Midden	Age	N	w-p (g)	$\frac{\text{N}}{\text{w-p}}$
FC 1	12,770 ± 140	20	86.9	0.23
FC 2	10,360 ± 80 9,380 ± 290	13	114.7	0.11
FC 5	9,700 ± 110	24	112.7	0.21
FC 4	6,100 ± 100	20	69.2	0.29
FC 7	3,740 ± 70	16	143.9	0.11
FC 6	3,550 ± 60	20	150.2	0.13
FC 9	2,260 ± 90	32	62.3	0.51
AC 7	11,130 ± 200	26	121.0	0.21
AC 8	10,140 ± 190	22	99.6	0.22
AC 9	10,070 ± 70	23	72.8	0.32
AC 1	10,030 ± 200 10,030 ± 330 9,600 ± 140	16	94.1	0.17
AC 2	7,200 ± 0	30	59.5	0.50
AC 6	3,400 ± 60	27	43.8	0.62
AC 5	3,000 ± 70	33	70.9	0.47
AC 4	1,820 ± 50	25	66.3	0.38

the needles from the Fishmouth Cave and Allen Canyon series are assigned here to limber pine, which occurs today in the Abajo Mountains.

Fishmouth Cave Sequence

The sequence for Fishmouth Cave (Fig. 5) spans vegetation changes from assemblages dominated by limber pine and Douglas fir (latest Pleistocene) to modern ones dominated by Utah juniper (see Table 9). FC 1, dated at 12,770 B.P., is the single Pleistocene midden from this locality. Trees and shrubs abundantly represented from this sample include *Pinus flexilis, Pseudotsuga menziesii, Cornus stolonifera, Juniperus communis, J. scopulorum, Cercocarpus montanus,* and *Rosa woodsii.* None of these are at the site today and the assemblage does not occur locally at elevations lower than 2438 m, representing a minimum displacement of ca 850 m. Three of the plants with relatively stable records from latest Pleistocene to the present are *Ephedra* sp., *Opuntia polyacantha,* and *Yucca angustissima.*

Two early Holocene middens (FC 2 and FC 5) from Fishmouth Cave record vegetation changes during the Pleistocene-Holocene transition. No longer at the site are *Picea pungens, Juniperus communis,* and *Rosa woodsii.* The older sample (FC 2) resembles the late Pleistocene midden in that it contains *Pinus flexilis, Juniperus scopulorum,* and *Cercocarpus montanus.* The younger midden (FC 5) may signal the initial development of modern vegetation; it lacks *Pinus flexilis, Juniperus scopulorum,* and *Cercocarpus montanus* and is in turn dominated by *Juniperus osteosperma.* Dated at 9700 B.P., FC 5 may represent the first arrival of *J. osteosperma* in the area of Fishmouth Cave. Macrofossils of *Quercus gambelii* were found only in the two early Holocene middens and a middle Holocene sample (FC 4). A marked decrease in *Pseudotsuga menziesii* is noted from FC 1 to FC 4 (Table 9). Aside from *Quercus gambelii* and *Juniperus osteosperma,* plants that first appear in the early Holocene include *Amelanchier utahensis, Rhus trilobata,* and *Cercocarpus intricatus.* The latter three species have relatively stable records for the rest of the Holocene.

The middle and late Holocene middens from Fishmouth Cave approximate the modern flora with a few notable exceptions. The middle Holocene sample differs from the late Holocene in that it contains *Pseudotsuga menziesii* and *Quercus gambelii.* Single needles of *Pseudotsuga* in FC 6 and FC 7 are probable contaminants from older middens. *Quercus gambelii* occurs today as a riparian tree in the ravine in front of the shelter, but beyond the probable collecting range of packrats. During the early and middle Holocene, Gambel oak probably grew on the exposed slope immediately in front of the shelter.

The two oldest late Holocene middens (FC 7 and FC 6) are characterized by high percentages of juniper macrofossils, at least double what they are in other middens from Fishmouth Cave (Table 9). This may reflect a local increase in the density of junipers. The only record of pinyon (*Pinus edulis*), which is not at the site today, is FC 7 (3740 B.P.). This record may reflect limited expansion of pinyon south along Comb Ridge, at a time when the density of junipers is also increasing in the immediate vicinity of Fishmouth Cave.

The youngest sample from Fishmouth Cave (FC 9; 2260 B.P.) is peculiar for a number of reasons. The greatest number of taxa from Fishmouth Cave is recorded in this midden (N = 32). One of the dominants, *Cowania mexicana,* appears in no other sample. FC 9 also contains the only records of *Shepherdia rotundifolia* and *Purshia tridentata.* The weight percentages for *Juniperus osteosperma* and *Opuntia polyacantha* closely resemble those for FC 5 (9700 B.P.).

Allen Canyon Cave Sequence

The rich macrofossil record from Allen Canyon Cave (Fig. 6) spans the last 11,300 years, with the vegetation at the site ranging from spruce-fir forest to stands dominated by *Pseudotsuga menziesii, Pinus ponderosa,* and *Pinus edulis.* A number of plants appear throughout the entire sequence. These include *Pseudotsuga menziesii, Pachystima myrsinites, Amelanchier utahensis,* and *Cornus stolonifera.* Two mosses, *Hypnum cupressiforme* and *Thuidium abietinum,* occur

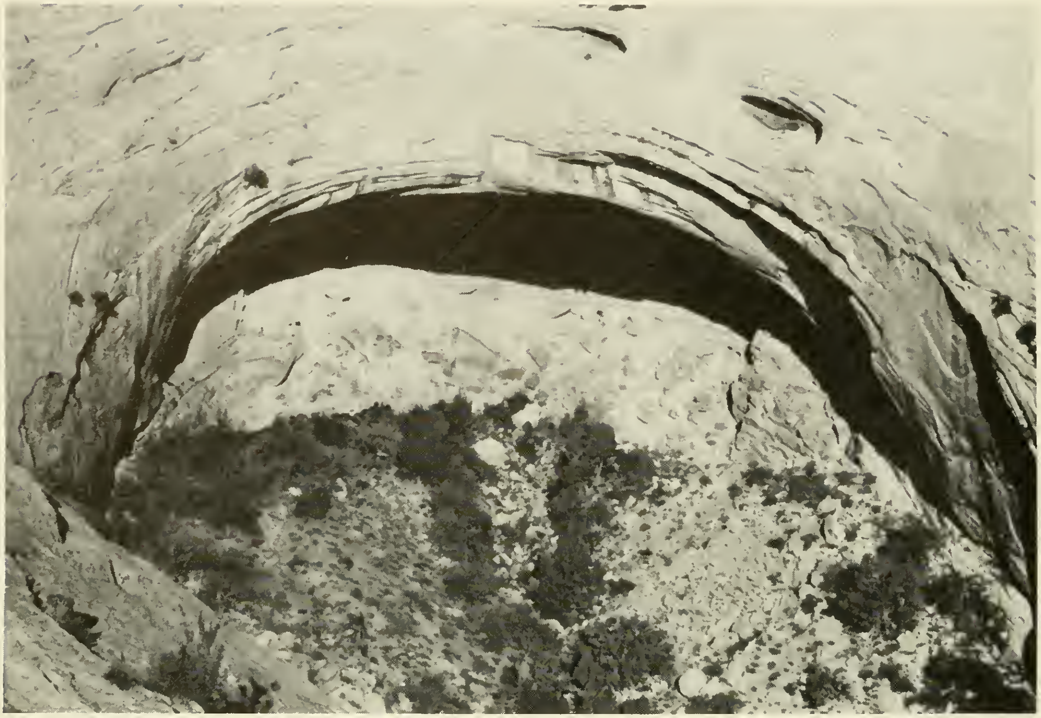

Fig. 3. View of Fishmouth Cave from ridge to the southeast, showing plant community directly in front of shelter. The larger trees and shrubs include Utah juniper (*Juniperus osteosperma*), single-leaf ash (*Fraxinus anomala*), Utah serviceberry (*Amelanchier utahensis*), and squawbush (*Rhus trilobata*).

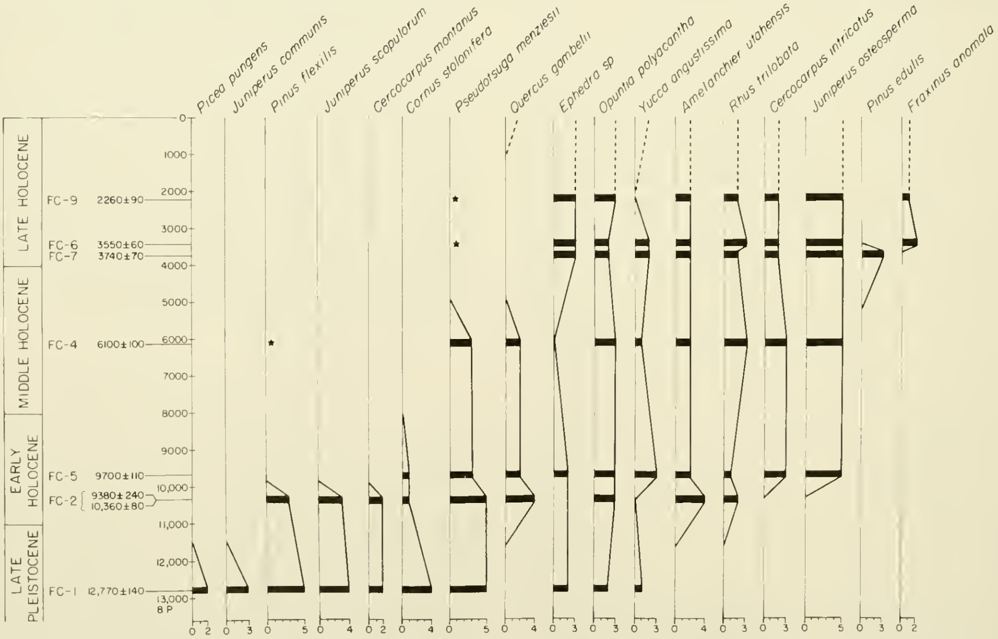

Fig. 5. Seriated chronosequence of select plant macrofossils and their relative abundances in fossil packrat middens from Fishmouth Cave, San Juan County, Utah. Sample points are joined by a straight line not to imply a continuous stratigraphic record, but to accentuate differences between samples. Asterisks indicate probable contaminants. Fishmouth Cave, San Juan County, Utah. 37°25′45″ N, 109°39′ W, elev. 1585 m (5200 ft).

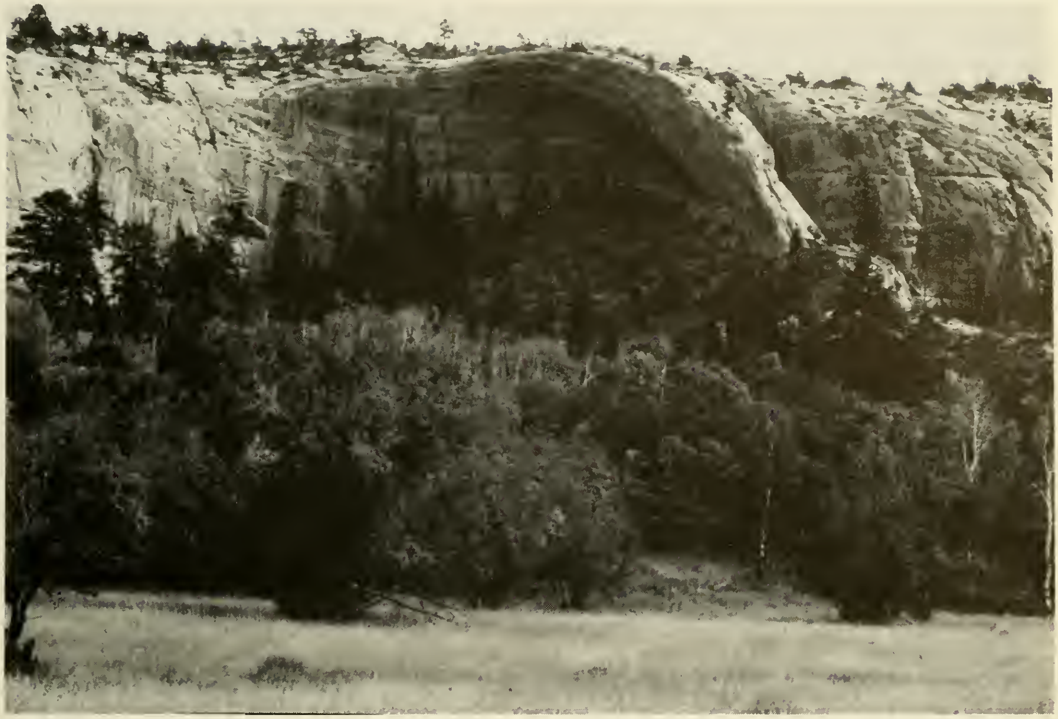

Fig. 4. View of Allen Canyon Cave from the unentrenched valley of an unnamed tributary of Allen Canyon. The larger trees in front of the shelter are Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*). A grove of aspen (*Populus tremuloides*) occupies the foreground. Scattered ponderosa pine trees occur in pinyon-juniper woodland on the ridge top.

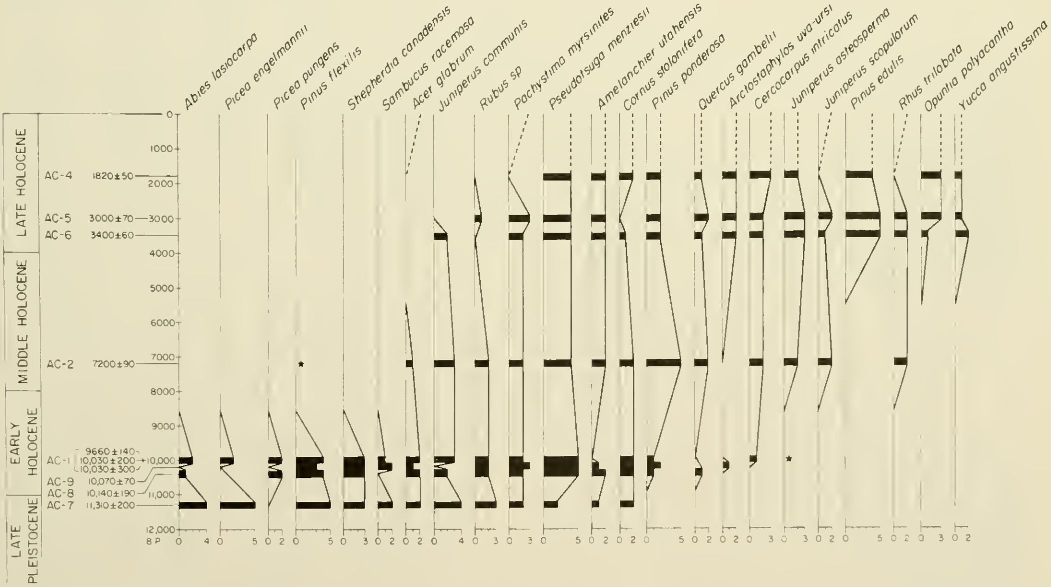

Fig. 6. Seriated chronosequence of select plant macrofossils and their relative abundances in fossil packrat middens from Allen Canyon, San Juan County, Utah. Sample points are joined by a straight line not to imply a continuous stratigraphic record, but to accentuate differences between samples. Asterisks indicate probable contaminants. Allen Canyon Cave, San Juan County, Utah, 37°47′30″ N, 109°35′30″ W, elev. 2195 m (7200 ft).

sporadically throughout the sequence, starting with the oldest sample. Both mosses, which have very large ecological amplitudes (Haring 1961), grow directly in front of the shelter today. The Allen Canyon sequence is characterized by major and rapid change in the overstory and remarkable stability in the understory of the cliffside communities.

The latest Pleistocene sample (AC 7: 11,310 B.P.) is dominated by *Picea engelmannii, Pinus flexilis, Abies lasiocarpa,* and *Juniperus communis. Pseudotsuga menziesii* is a relatively unimportant plant in this assemblage (Table 9). This sample also contains a few specimens of *Bromus anomalus, Trisetum spicatum,* and *Deschampsia caespitosa,* which are common grasses in subalpine to alpine meadows. The assemblage from AC 7 suggests a modern analog at ca 2896 m at the lower limits of Engelmann spruce–alpine fir forest.

The three early Holocene middens (AC 8, AC 9, AC 1) were all dated at ca 10,000 B.P. and record significant changes from the late Pleistocene. Table 12 shows an enormous reduction in the weight percentages for *Picea* spp., *Abies lasiocarpa,* and *Juniperus communis. Pinus flexilis* also decreases by a factor of three, whereas there is a 10- to 40-fold increase in the abundance of *Pseudotsuga menziesii.* One of the more interesting developments is the replacement of *Picea engelmannii* by the lower elevation *P. pungens,* indicating an upward shift in vegetation zones. *Shepherdia canadensis, Acer glabrum,* and *Sambucus racemosa* retain their importance from the late Pleistocene. Significant new arrivals include *Pinus ponderosa, Quercus gambelii,* and *Cercocarpus intricatus.* A single *Juniperus osteosperma* twig in AC 1 may be a contaminant from younger material in the shelter. With a few exceptions, the

Table 9. Weight percentages for select plant taxa in fossil packrat middens from Fishmouth Cave (FC) and Allen Canyon Cave (AC), San Juan County, Utah. Weight percentages obtained by dividing the total weight of macrofossils from one species by the total weight of the plant matrix in the midden (see Table 3), and then multiplying by 10. T = trace fossils, one or two items of insufficient weight, possible contaminants.

	12,770 ± 140	10,360 ± 80 9,380 ± 290	9,700 ± 110	6,100 ± 100	3,740 ± 70	3,550 ± 60	2,260 ± 90
Fishmouth Cave	FC 1	FC 2	FC 5	FC 4	FC 7	FC 6	FC 9
Pinus edulis					0.16		
Opuntia polyacantha	0.16	0.40	1.15	0.31	0.13	0.21	0.99
Juniperus osteosperma			8.47	12.19	21.49	26.49	7.81
Quercus gambelii		0.47	T	0.89			
Pseudotsuga menziesii	10.24	7.20	1.11	0.50		T	T
Pinus flexilis	12.38	0.50		T			
Juniperus scopulorum	0.28	2.10					
Juniperus communis	0.48						

	11,130 ± 200	10,140 ± 190	10,070 ± 70	10,030 ± 200 10,030 ± 330 9,600 ± 140	7,200 ± 90	3,400 ± 60	3,000 ± 70	1,820 ± 50
Allen Canyon Cave	AC 7	AC 8	AC 9	AC 1	AC 2	AC 6	AC 5	AC 4
Opuntia polyacantha						T	0.33	0.31
Pinus edulis						5.34	3.25	2.11
Juniperus osteosperma				T	0.19	2.23	1.53	0.12
Pinus ponderosa		T	0.22	T	5.04	0.06	0.14	0.06
Pseudotsuga menziesii	0.14	3.49	1.54	6.05	1.98	1.43	1.18	1.87
Juniperus communis	1.00	0.02		0.25	0.20	0.11		
Pinus flexilis	4.49	2.30	1.27	1.79	T			
Picea sp.	5.61	0.09	0.16	0.09				
Abies lasiocarpa	1.98	T		0.03				

early Holocene assemblages from the Allen Canyon locality resemble the late Wisconsin midden from Fishmouth Cave. Differences include the presence of *Ephedra* sp., *Yucca angustissima*, and *Opuntia polyacantha* at the lower site, and the richer assemblage of understory shrubs (*Shepherdia canadensis, Acer glabrum, Pachystima myrsinites*, and *Rubus* sp.) at the higher site.

The single middle Holocene sample (AC 2) indicates a major turnover in the local flora between 10,000 and 7200 B.P. Judging from the chronology at Fishmouth Cave, this change may have happened between 9000 and 10,000 B.P. Plants that drop out of the record completely include *Abies lasiocarpa, Picea* spp., *Pinus flexilis* (see comments below), *Shepherdia canadensis*, and *Sambucus racemosa*. The single *Pinus flexilis* needle may be a contaminant from an early Holocene midden (AC 1) just a few meters away on the floor of the shelter. New arrivals at Allen Canyon Cave are *Juniperus osteosperma, J. scopulorum*, and *Rhus trilobata*. Surprisingly, the dominant in the late Holocene middens, *Pinus edulis*, is absent from AC 2. Instead, this midden contains from 20 to 40 times as much *P. ponderosa* as any of the early and late Holocene middens (Table 9).

Three middens (AC 6, 3400 B.P.; AC 5, 300 B.P.; and AC 4, 1820 B.P.) record the modernization of the local flora. Between 7200 and 3400 B.P., *Acer glabrum* drops out of the sequence. It occurs today alongside *Populus tremuloides* in the steep drainage just below the shelter. Probably within the last few millennia, this drainage eroded upstream, leaving the shelter perched 50 m above moist, riparian habitats where *Acer glabrum* thrives. The increased vertical distance from the mouth of the shelter to the steep headcut may explain the absence of *Acer glabrum* in the latter part of the sequence. Records for *Juniperus communis, J. scopulorum*, and *J. osteosperma* are quite variable during the late Holocene. All three occur in the oldest of the three middens (AC 6). *Juniperus communis* is missing from the two youngest middens (AC 5 and AC 4), which contain both *J. scopulorum* and *J. osteosperma*. The most recent sample only has *J. osteosperma*. New plants that arrive in the late Holocene include *Pinus edulis, Opuntia polyacantha, Yucca angustissima*, and *Oryzopsis hymenoides*. The appearance of these plants in the Allen Canyon sequence may signal the middle Holocene expansion of xeric woodlands at higher elevations.

Biogeographic and Paleoclimatic Considerations

A relatively high number of endemic plants (70) has been reported for the Colorado Plateaus (Welsh 1978). According to Reveal (1979), this is the result of historical stability and isolation due to imposing physiographic barriers of mountains and high plateaus. Two corridors that may have permitted plant migration are the relatively low divide between the San Juan and Rio Grande rivers and the Dixie Corridor between the Grand Canyon and the Utah Plateaus. Reveal (1979) believes that, in the Great Basin, Pleistocene compression of low vegetation zones between the base of the mountains and pluvial lakes on the valley floors extirpated many low-elevation plants. Holocene retreat of the shorelines exposed large areas for plant colonization, particularly by halophytes. Because there were no large pluvial lakes on the Colorado Plateaus, Reveal (1979) maintains that the existing vegetation was not significantly pushed out of the area during the Pleistocene.

There are several problems with Reveal's interpretation for the high number of endemics on the Colorado Plateaus. I have already demonstrated a minimum lowering of 700–850 m for subalpine trees along the Abajo Mountains–Comb Ridge gradient. Late Pleistocene records of *Picea pungens, Pinus flexilis*, and *Juniperus communis* down to 1585 m suggest that both the pinyon-juniper woodland and the modern desert-scrub zones were displaced far to the south and west. I seriously doubt that either zone existed upstream of the confluence (1040 m) of the San Juan and Colorado rivers. The high number of endemic species of milkvetches (*Astragalus* sp.), mostly from low elevations, gives the appearance that the majority of endemic plants are today restricted to desert sites at lower elevations. However, almost half of the endemics on the Colorado Plateau now occur above 1980 m. The decrease in area with elevation translates into a greater density of endemics at higher than lower elevations (Welsh 1978). Pleistocene lowering of montane communities probably increased the area occupied by these higher-elevation endemics. Elevations above 2130 m, mostly clad in spruce-fir forest and alpine tundra, would have served as effective barriers to the migration of plants now occurring at intermediate elevations. In southeastern Utah, many of today's low-elevation endemics probably grew alongside subalpine and montane conifers, or in *Artemisia* steppe, during the late Wisconsin. Postglacial competition with new arrivals better adapted to xeric conditions may have forced endemics either upslope or to poorer substrates (e.g., Mancos Shale) where competition is less intense.

Similar lowering of vegetation zones has been documented elsewhere on the Colorado Plateaus. At Cowboy Cave (1770 m) in nearby Wayne County, cave sediments dated to between 11,000 and 13,000 B.P. yielded macrofossils of both *Picea pungens* and *P. engelmannii* (Spaulding and Peterson 1980, species determination by O. K. Davis). During the full-glacial period (21,000–15,000 B.P.) in the eastern Grand Canyon, several conifers, including *Pseudotsuga menziesii*, *Juniperus communis*, *Abies concolor*, *Picea engelmannii*, and *Pinus flexilis* expanded 600–1000 m below their modern ranges (Cole 1982). At 1700 m in Canyon de Chelly, northeastern Arizona, a packrat midden dated at 11,900 B.P. contains *Picea pungens*, *Pinus flexilis*, *Juniperus communis*, and *Pseudotsuga menziesii* (Betancourt and Davis 1984). *Pinus flexilis* no longer occurs in the nearby Chuska Mountains, which rise just slightly above 2740 m.

Depression of these montane and subalpine elements resulted from relaxation of the limiting factors in effect at their lowest elevations, mainly drought and possibly competition. At the lower limits of a plant, high temperatures and deficient soil moisture produce transpirational stress for established individuals and reduce the potential for germination and seedling establishment. Relaxation of these controls can be accomplished most readily by lowering summer temperatures and increasing precipitation for critical times of the year. Table 10 compares modern climates at Fishmouth and Allen Canyon caves with climates for their late Wisconsin analogs at higher elevations. The reconstructed values for the elevations of the caves (1585 and 2195 m) are probably reasonable estimates. Because the regressions (Fig. 1) include only

Table 10. Precipitation and temperature predicted from elevations of Fishmouth Cave, Allen Canyon Cave, and the modern elevational analogs for late Wisconsin midden assemblages at the two sites. Linear regression equations used to calculate these values are presented in Figure 2. The elevational analog approach ignores possible shifts in the seasonal distribution of rainfall. Such shifts may in effect alter environmental lapse rates. Annual means are for the hydrological year (October–September) with winter means from October to March and summer from April to September.

	Fishmouth Cave	Modern analog for FC 1	Percent increase in ppn or cooling in degrees C	Allen Canyon Cave	Modern analog for AC 7	Percent increase in ppn or cooling in degrees C
Elevation (m)	1585	2438	–	2195	2896	–
Winter ppn (mm)	124	201	62%	179	242	35%
Summer ppn (mm)	108	176	62%	157	212	35%
Annual ppn (mm)	232	377	62%	336	452	35%
Winter temperature (C)	3	0	3 C	1	-1	2 C
Summer temperature (C)	19	14	5 C	15	11	4 C
Annual temperature (C)	11	7	4 C	8	5	3 C

stations below 2080 m, predicted climates for higher elevations should be taken as minimum estimates based on unusually low vertical gradients. Using these conservatively low rates, calculations based on elevational analogs represent roughly 35 to 60 percent more rainfall than today. For comparison, I recalculated the precipitation-elevation regressions to include data from Camp Jackson (2804 m), Buckboard Flats (2865 m), and La Sal Mountains (2865 m). Application of the steeper gradients suggests a 50 to 120 percent increase over modern rainfall. The difference between the predictions for Allen Canyon Cave as opposed to Fishmouth Cave does not necessarily imply that rainfall increased more at lower than at higher elevations. I posit that the lower limits of Engelmann spruce–alpine fir were in Cottonwood Wash down to 1830 m (a 60 percent increase using the lower rates).

Seasonal gradients (and thus annual rates) may be quite different today than during the late Wisconsin. For the middle Holocene, Davis et al. (1980) incurred a change in seasonal gradients to explain unequal displacement of spruce and fir in the White Mountains of New Hampshire. Most reconstructions of late Pleistocene climate in the western United States call for increases in winter rainfall (Van Devender and Spaulding 1979, Spaulding et al., in press). Though not yet demonstrated with historical data, the steeper gradients in precipitation probably occur in winter when snowfall is disproportionately high at upper elevations. Judging from the absence of plants that respond primarily to summer moisture, late Wisconsin summers might have been much drier than today. Hence, the seasonal breakdown of predicted values in Table 10 should be taken as a first approximation that considers the seasonal relation of precipitation with temperature in respect to effective moisture at the various elevations. This analog approach suggests a 4 C cooling of mean annual temperatures during the late Wisconsin at Fishmouth Cave and a lesser 3 C lowering for the Allen Canyon locality. The more significant differences are in summer temperatures (4–5 C) as opposed to winter (1–2 C). At Fishmouth Cave, the presence of *Opuntia polyacantha* and *Yucca angustissima* in the late Wisconsin assemblage suggests that the winters were moderate. Neither occurs today above 2740 m in the Abajo Mountains or other local ranges. Also, neither species appears in the Allen Canyon sequence until 3400 B.P. If we can assume that *Opuntia polyacantha* and *Yucca angustissima* are rare where mean annual temperature dips below 6 C, the estimated value for 2740 m, it is unlikely that annual temperatures were lowered by much more than 5 C. A regional cooling greater than this (with little or no increase in rainfall) is proposed by several authors to explain Wisconsin depressions of 1000 m for orographic snowline, cryogenic deposits, and timberlines (Brakenridge 1978, Galloway 1970).

There are several pitfalls to the elevational analog approach. By definition, a depression in vegetation zones implies both increases in precipitation and decreases in temperature. Theoretically, observed depressions can be explained through increases in effective soil moisture induced by (1) increased rainfall alone, (2) cooler temperatures alone, or (3) some combination of the two. Planting of spruce in suburban landscapes of Denver, Colorado and Albuquerque, New Mexico (both at ca 1585 m elevation), gives the first tenet some credibility. Brakenridge (1978) illustrates the second example by citing a latitudinal analog for junipers found in packrat middens from the Sonoran and Chihuahuan Deserts. These same junipers grow at similar elevations along the Snake River Plain of southern Idaho, where precipitation is the same or less, but temperature is 8 C cooler than the fossil sites (see objections by Wells 1979). The third possibility, involving both parameters, is the most difficult to model. Environmental lapse rates combine along elevational gradients to produce rates of change in effective moisture and, thus, the advantage of elevational analogs.

The estimates derived from the southeastern Utah data differ from paleoclimatic reconstructions derived from packrat midden sequences in the Great Basin. The midden record shows that *Pinus flexilis* and *P. longaeva* expanded down to low elevations (1525–2070 m) throughout the Great Basin. These are the only two subalpine conifers present today in the central and southern

Great Basin. Displacements of *Picea engelmannii* and *Juniperus communis* have been documented at the more northerly sites, but records of *Pseudotsuga menziesii* and *Abies concolor* are present only in the eastern and southern Great Basin (Thompson and Mead 1982). The moisture requirements for *Pinus longaeva* and *P. flexilis* are considerably less than for other subalpine and montane conifers. Expansion of *P. longaeva* and *P. flexilis* in the absence of other mesophytic conifers has been used to imply cold and dry conditions for the Great Basin (Thompson and Mead 1982). Conversely, mesophytic conifers such as *Picea* spp., *Abies* spp., and *Pseudotsuga menziesii* were able to expand down to low elevations on the Colorado Plateaus. The two paleoclimatic reconstructions are not necessarily at odds, since they approximate the present east-to-west gradient in increasing aridity.

In both the Great Basin and the Colorado Plateaus, depressions of subalpine conifers may have been enhanced by a lack of competition with conifers prevalent today in lower montane forests and xeric woodlands. North of 36°N latitude, macrofossil evidence for *Pinus edulis*, *P. monophylla*, and *P. ponderosa* is scanty for the Pleistocene. *Pinus monophylla* occurred at ca 11,600 B.P. (1850 m) in the Sheep Range of southern Nevada (36°30'N) (Spaulding 1981). Isolated Pleistocene records of pinyon occur in the western Grand Canyon: the unconsolidated packrat layer at Rampart Cave (535 m); a packrat midden dated at 12,650 B.P. from 635 m elevation (Phillips 1977), and another midden dated at 16,580 B.P. from the Cave of the Early Morning Light at 1300 m elevation (Van Devender and Spaulding 1979). Aside from these records, pinyon is missing from over 70 Pleistocene middens collected between 425 and 2050 m throughout the Grand Canyon (Van Devender and Mead 1976, Van Devender et al. 1977, Phillips 1977, Mead 1981, Mead and Phillips 1981, Mead 1983, Cole 1982). Cowboy Cave (1770 m) has also yielded pinyon macrofossils of possible Pleistocene age, though the chances for contamination from rodent burrowing in the cave sediments are high. Traces of *P. edulis* were identified at Cowboy Cave from Unit 1b dated to between 13,000 and 11,000 B.P. (Spaulding and Peterson 1980). Significantly, pinyon was not found in the overlying Units II and III dated to between 8700 and 6400 B.P. Aside from the trace amounts in Unit I, pinyon first appears in sediments associated with a date of 3600 B.P. (Hewitt 1980). The Pleistocene record from Cowboy Cave is equivocal until a direct date on pinyon can be obtained.

The only Wisconsin-age macrofossils of *Pinus ponderosa* anywhere in the Southwest are from the Santa Catalina Mountains of southern Arizona (Thompson and Van Devender 1982). *Pinus ponderosa* and *P. edulis* arrive at Chaco Canyon, New Mexico (1920 m), between 9500 and 8300 B.P. (Betancourt et al. 1983). *Pinus ponderosa* is recorded at the Allen Canyon locality as early as 10,140 B.P., and *P. edulis* occurs only in samples younger than 7200 B.P. For the Colorado Plateaus, the present distributions of both species were probably achieved during the Holocene. *Pinus edulis* probably migrated into the Plateaus from Pleistocene woodlands in the Chihuahuan Desert (Van Devender et al., in press). It remains unclear whether *P. ponderosa* migrated from the south with the onset of postglacial conditions or simply expanded from small populations in local mountain ranges. The absence of *P. ponderosa* and *P. edulis* in the Pleistocene may have facilitated low elevation expansion of other montane and subalpine conifers, primarily through competitive release. This may ultimately explain the disharmonious association of subalpine conifers with xerophytic plants common today in ponderosa pine and pinyon-juniper woodlands.

Absence of *P. ponderosa* and *P. edulis* from the Plateaus during the late Wisconsin is climatically significant. Pearson (1950) notes that regeneration of *P. ponderosa* is sporadic because favorable distribution of summer rainfall must be combined with a productive seed year. Its reproductive success in the Southwest depends largely on the predictability of abundant summer rainfall. Once established, the seedlings are capable of withstanding drought, with soil moisture content near or even below wilting point, enabling them to survive at lower altitudes than other associated conifers (Fowells and Kirk 1945). *Pinus edulis* and *Quercus gambelii*, the latter a frequent associate in pinyon-juniper woodlands and ponderosa pine forests, presently terminate their northern ranges at ca 41°N latitude. Neilson and Wullstein (1983) suggest that the northern limits of both species result from low rates of reproduction and seedling survival due to the greater frequency of spring freezes and summer droughts with increasing latitude. Macrofossils of *Quercus gambelii* first appear in the Allen Canyon and Fishmouth Cave localities during the early Holocene. A midden of similar age from Canyon de Chelly, northeastern Arizona, contains no oak pollen (Betancourt and Davis 1984). However, both macrofossils of *Q. gambelii* and oak pollen have been identified from a late Wisconsin dung layer in a cave (1340 m) along the Waterpocket Fold, about 100 km west of Comb Ridge (O. K. Davis, pers. comm.). These data imply that *Q. gambelii* may have been restricted to lower elevations at the northern edge of its late Wisconsin range.

Another interesting species that is missing from the late Wisconsin at Fishmouth and Allen Canyon caves is *Juniperus osteosperma*. This juniper is a common element in Pleistocene middens from 2070 m down to 425 m in the Grand Canyon (Cole 1982, Phillips 1977). Its arrival at Fishmouth Cave ca 9700 B.P. probably signals its Holocene expansion north and east of the Grand Canyon. A similar expansion of its close relative *J. monosperma* probably occurred north and west of the Chihuahuan Desert into the eastern portion of the Colorado Plateaus. The modern ranges of the two overlap along a strip from east central Arizona into western Colorado. During the late Wisconsin both the northern and eastern limits of *Juniperus osteosperma* were probably in the vicinity of the Grand Canyon. *Juniperus monosperma* probably did not range far north of 34°N latitude in New Mexico (Van Devender et al., in press). Expansion of *J. osteosperma* might have been rapid, with midden records as early as 10,000 B.P. from the Pryor Mountains in Montana (J. I. Mead, pers. comm.). The oldest record of *J. monosperma* from Chaco Canyon is 8300 B.P. (Betancourt et al. 1983).

For the Wisconsin, range contractions to the south may be related to a southerly displacement of the polar jet stream and Mitchell's (1976) "winter" boundary. Such a displacement has been proposed by a number of authors from paleovegetation data (Van Devender and Spaulding 1979), general circulation models (Bryson and Wendland 1967), and modern plant distributions (Neilson and Wullstein 1983). In southeastern Utah, a southerly displacement of the jet stream and midlatitude storm track would result in greater winter and less summer precipitation, cooler summer temperatures, and a higher incidence of spring freezes than today. If the reasoning of Bryson and Wendland (1967) is to be followed, large decreases in winter temperatures were prevented by the presence of the North American ice sheets. They argue that the high plateaus of ice blocked incursions of cold, low level Arctic air from entering the United States. Air flow from the ice caps would have been mostly katabatic, producing mild winters over the North American continent.

The early Holocene on the Colorado Plateaus appears to have been a time of rapid changes in vegetation. At Fishmouth Cave, two major shifts in the flora occurred in quick succession. Between 12,770 and 10,000 B.P., both *Picea pungens* and *Juniperus communis* dropped out of the sequence, with *Pinus flexilis* and *Juniperus scopulorum* following suit soon after 10,000 B.P. New arrivals in the early Holocene of Fishmouth Cave included *Quercus gambelii* and *Juniperus osteosperma*. At Allen Canyon Cave, again there were two shifts during the early part of the sequence. *Picea engelmannii* and *Abies lasiocarpa* retreated to higher elevations between 11,300 and 10,000 B.P., leaving *Pinus flexilis* and *Pseudotsuga menziesii* as the dominants. The initial change toward the modern flora at the site occurred between 10,000 and 7200 B.P. A similar change happened between 9500 and 8300 B.P. at Chaco Canyon, which is intermediate in elevation (1920 m) between the two sites. At all three sites, plants associated with summer precipitation and relatively high annual temperatures (*Quercus gambelii, Pinus ponderosa, Pinus edulis, Juniperus monosperma, J. osteosperma,* etc.) began arriving at ca 10,000 B.P. *Pinus edulis* is not recorded at either Fishmouth or Allen Canyon caves until the late Holocene, but this may result from location of the sites at the lower and upper ends of modern pinyon-juniper woodland.

The timing of these rapid vegetation changes during the early Holocene in southern Utah is very similar to the Swan Lake pollen and macrofossil records on the Idaho-Utah border (Bright 1966). Both records are interpreted as representing a progressive decrease in effective moisture, either due to warmer temperatures and/or reduced rainfall, for the latest Pleistocene. However, effective moisture during the early Holocene is interpreted as being higher than today. During the latter part of the period there appears to have been a change in the seasonal distribution of rainfall, signalling the onset of monsoonal conditions for the Colorado Plateaus. The use of elevational analogs may not apply, since a major reorganization of vegetation zones occurred during this period. These results are interesting in light of the general circulation model recently proposed for 9000 B.P. (Kutzbach 1981, Kutzbach and Otto-Bliesner 1982), and location of the southeastern Utah sites along the present monsoonal boundary. The model uses increases in solar radiation for June-July-August in 9000 B.P. to power land-ocean temperature contrasts and intensified monsoonal circulation. Paleoclimatic data from Africa and Asia closely agree with the model's prediction for intensified summer monsoons during the early Holocene, but the model has not been applied to North America because of difficulties in assessing the role played by the ice sheets.

There is general agreement that global temperatures were warmer during the middle Holocene (ca 8000-4000 B.P.) than today. In the western U.S., a great deal of controversy has revolved around whether this period was drier or wetter than now. The argument seems to be over the relative amounts of summer precipitation. The concept of a hot-dry "Altithermal" (7500-4000 B.P.) was formulated by Antevs (1955) from work in the northern Great Basin, which is beyond monsoonal influences. Widespread application of the Altithermal concept across the western U.S., regardless of regional variability in climate, has been called into question. Martin (1963) first argued that warmer conditions might enhance the effectiveness of the summer monsoons south and east of the Great Basin. Although considerable data have since been applied to this issue, the controversy remains unresolved.

Warmer temperatures for the middle Holocene have been suggested from modern distributions of relic hybrids between *Quercus gambelii* and *Q. turbinella* (Cottam et al. 1959). The deciduous *Q. gambelii* is better adapted to cold winter temperatures than the evergreen *Q. turbinella*. Leaves of the hybrid remain until late fall, long after *Q. gambelii* has dropped its leaves. I agree with Cottam et al. (1959) that neither oak could have persisted in north central Utah during the Wisconsin glaciation. Both species probably expanded into this area during the middle and late Holocene, with the hybrid isolated from *Q. turbinella* with decreasing temperatures during the Neoglacial. A similar expansion and contraction in the range of *Pinus edulis* and *P. monophylla* may account for ecotonal hybrids north and west of the present range of *P. edulis* (Lanner 1974).

In general, the records from both Allen Canyon and Fishmouth Cave indicate greater effective moisture during the middle and early part of the late Holocene (before 3000 B.P.). At Fishmouth Cave, the extralocal and mesophytic *Pseudotsuga menziesii* occurs in a sample dated at 6100 B.P., but I cannot ascertain that it is not a contaminant from older deposits. Around 3700-3500 B.P., pinyon-juniper woodlands might have expanded into lower elevations along Comb Ridge, as indicated by high macrofossil percentages for *Juniperus osteosperma* and macrofossils of the extralocal *Pinus edulis*. At Allen Canyon Cave, the pattern is similar. *Pinus ponderosa* achieved by far its highest macrofossil percentages in a midden dated at 7200 B.P. A sample dated at 3400 B.P. contains the youngest macrofossils of the extralocal *J. communis*. *Juniperus scopulorum* appears in all middle and late Holocene middens except the youngest at 1820 B.P., which only contains the more xerophytic *J. osteosperma*. The arrival of *Pinus edulis*, *Opuntia polyacantha* and *Yucca angustissima* in the late Holocene may also denote a greater aridity for the site than during the middle Holocene. At both sites, the youngest middens (1800-2200 B.P.)

best approximate the modern floras. The midden record from southeastern Utah suggests that the modern elevational range of local plants was not achieved until very recently.

Summary

Packrat midden sequences from two caves record vegetation changes from the late Wisconsin through late Holocene in the central portion of the Colorado Plateaus. The two sites are separated vertically by 610 m in elevation along a more or less continuous gradient of Navajo Sandstone from Comb Ridge into the Allen Canyon country of the Abajo Mountains. Fishmouth Cave (1585 m) is located in Utah-juniper grassland just below and south of pinyon-juniper woodland. Allen Canyon Cave (2195 m) occupies an area intermediate between mesa top pinyon-juniper woodland and cliffside stands of Douglas fir, ponderosa pine, and aspen. The midden sequences trace the development of modern plant zonation from the much-displaced vegetation of the late Wisconsin. Local environmental lapse rates are used to calculate the differences between late Wisconsin and modern climates. The similar intervals encompassed at each site allow simultaneous views of vegetation change at low and intermediate elevations. Comparison with other midden sites from the Colorado Plateaus and adjacent areas yields a rough sketch of past biogeography. The distributions of several important plants are related to changes in the position of air mass boundaries over northern and southern Utah.

The latest Pleistocene record calls for minimum elevational depressions of 700–850 m for subalpine and upper montane plants. At Allen Canyon Cave, spruce-fir forest dominated by *Abies lasiocarpa, Picea engelmannii, Pinus flexilis,* and *Juniperus communis* was depressed from its lower limits today at ca 2896 to 2195 m. *Picea pungens, Pinus flexilis,* and *Juniperus communis* occur in the late Wisconsin midden from Fishmouth Cave, suggesting an elevational analog above 2438 m. The analog approach predicts a 3–4 C cooling from present mean annual temperatures. Records of *Opuntia polyacantha* and *Yucca angustissima* at Fishmouth Cave argue against late Wisconsin cooling exceeding 5 C. Mean annual precipitation is estimated at from 35 to 60% greater than today. Potential error in the use of elevational analogs for quantitative climatic estimates is recognized. The analog approach dictates both increases in precipitation and decreases in temperature to produce greater effective moisture. Concentration of climatic stations at lower elevations, for instance, means that the steeper rates of temperature decrease and precipitation increase in the upper mountain belts are ignored. The minimum estimates for climatic change are probably reasonable considering that depression of subalpine and upper montane conifers was probably enhanced by the absence of *Pinus ponderosa* and *Pinus edulis.*

The early Holocene at the two sites appears to represent a major reorganization in local plant communities. Beginning ca 10,000 B.P., several plants now dominant in the area began to arrive. These include *Pinus ponderosa, Quercus gambelii,* and *Juniperus osteosperma. Pinus edulis* was a rather late arrival (in the middle Holocene), but this may reflect the location of the two sites at its upper and lower limits. In nearby Chaco Canyon, New Mexico, this pygmy conifer arrived sometime between 9500 and 8300 B.P. Pinyon probably arrived in the middle of its elevational range between 10,000 and 8,000 B.P. and failed to fully expand to its present elevational range until the middle and late Holocene. A case is made for the early Holocene climate to involve a northward displacement of the polar jet stream and middle latitude storm track following its southerly position during the late Wisconsin. The upward migration of subalpine and upper montane elements coupled with the arrival of plants formerly displaced to the south is interpreted to mean increased summer as well as mean annual temperatures, a decreasing frequency of spring freezes, and a shift from winter to summer-dominant rainfall. The present monsoonal boundary began to approach its present position between 10,000 and 8000 B.P. A model calling for increased summer temperatures and intensified summer monsoons during the middle Holocene is suggested by the midden records. Greater effective moisture than present is inferred at both

sites. The modern vegetation at the sites is not fully in place until ca 2000 B.P.

Based on these new data from southeastern Utah, I envision the scope of future midden studies on the Colorado Plateaus to be as follows. A network of midden localities should be established at the southern end of the Plateaus to delineate the late Wisconsin northern limits of such hallmark plants as ponderosa pine, pinyon pine, one-seed juniper, and Gambel oak. Midden sequences from the northern part of the Plateaus in north central Utah and northern Colorado can be used to determine the arrival times at the northernmost stations for these species. Holocene rates of migration can thus be extrapolated. It is also possible that several of these plants expanded beyond their present northern limits as a consequence of a warming trend during the middle Holocene. This is directly testable with development of new midden sequences at critical localities. Data from Fishmouth and Allen Canyon caves also point up an interesting possibility that plants migrating into an area arrive first into the middle of their elevational range. A lag time of several millenia may separate the first arrival of a species and expansion into its full elevational range.

Quantitative estimates of climatic change are a desirable, if sometimes untenable, aspect of paleoecology. Specifically, strategies such as the use of elevational analogs are fraught with the inability to independently estimate changes in temperature or precipitation. Many of the arguments based on shifts in the elevational range of plants can be reduced to fluctuations in effective moisture. That is, greater effective moisture results from either lowered temperatures, increased rainfall, or some combination of both. One approach is to develop ways of assessing temperature changes independent from rainfall. The temperature signal from ratios of stable isotopes ($^{18}O/^{16}O$; $^{13}C/^{12}C$; D/H) in meteoric water suggests one possibility that is currently being tested. In general, isotope ratios in meteoric water reflect the temperature at the site of precipitation (the lower the temperature the smaller the isotopic ratio). Natural systems which record variations in these ratios through time should preserve a record of past temperature fluctuations. One such system is represented in plants (Epstein et al. 1976). Conversion of cellulose from plant macrofossils to water and measurement of its isotopic composition should yield an assessment of temperature for the specific fossil locality. Measurement of isotopic ratios from packrat midden macrofossils is already underway. Arnold (1979) demonstrates that the approach is viable for oxygen isotope ratios in juniper from Sonoran Desert middens. A more recent experiment with a lengthy sequence of middens from the Great Basin show an even greater sensitivity (Siegel 1983). In the near future, I anticipate that single-site sequences, such as are described here for Fishmouth and Allen Canyon Caves, will be specifically targeted for the measurement of stable isotopic ratios and reconstruction of paleotemperature curves, independent from precipitation.

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LITERATURE CITED

ANTEVS, E. 1955. Geologic climatic dating in the West. Amer. Antiquity 20:317–335.

ARNOLD, L. 1979. The climatic response in the partitioning of the stable isotopes of carbon in junipers from Arizona. Unpublished dissertation. University of Arizona, Tucson. 209 pp.

BAKER, F. S. 1944. Mountain climates of the western United States. Ecol. Monogr. 14:129–133.

BARRY, R. G., AND R. S. BRADLEY. 1976. Historical climatology. *In* H. W. Steinhoff and J. D. Ives, Ecological impacts of snowpack augmentation in the San Juan Mountains, Colorado. San Juan Ecology Project, Final Report, Fort Collins, Colorado State Univ. Publications, 43–67 (PB 255 012 NTIS), U.S. Dept. of Commerce, Springfield, Virginia.

BETANCOURT, J. L., AND O. K. DAVIS. 1984. Packrat middens from Canyon de Chelly, northeastern Arizona: paleoecological and archeological considerations. Quat. Res. 21:56–64.

BETANCOURT, J. L., P. S. MARTIN, AND T. R. VAN DEVENDER. 1983. Fossil packrat middens from Chaco Canyon, New Mexico: cultural and ecological significance. Pages 207–217 *in* 1983 Amer. Geomorphological Field Group Guidebook.

BETANCOUT, J. L., AND T. R. VAN DEVENDER. 1981. Holocene vegetation in Chaco Canyon, New Mexico. Science 214, 656–658.

BLEICH, V. C., AND O. A. SCHWARTZ. 1975. Observations on the home range of the desert woodrat, Neotoma lepida intermedia. J. Mamm. 56:518–520.

BRAKENRIDGE, G. R. 1978. Evidence for a cold, dry full-glacial climate in the American Southwest. Quat. Res. 9:22–40.

BRIGHT, R. C. 1966. Pollen and seed stratigraphy of Swan Lake, southeastern Idaho. Tebiwa 9:1–47.

BRYSON, R. A. 1966. Air masses, streamlines, and the boreal forest. Geog. Bull. 8:228–269.

BRYSON, R. A., AND W. D. LOWRY. 1955. The synoptic climatology of the Arizona summer precipitation singularity. Bull. Amer. Meteor. Soc. 36:329–339.

BRYSON, R. A., AND W. M. WENDLAND. 1967. Tentative climatic patterns for some late glacial and postglacial episodes in central North America. Pages 271–298 *in* W. J. Mayer-Oakes, Life, land and water, Univ. of Manitoba Press, Winnipeg.

COLE, K. L. 1981. Late Quaternary environment in the eastern Grand Canyon: vegetational gradients over the last 25,000 years. Unpublished dissertation. Univ. of Arizona, Tucson. 170 pp.

———. 1982. Late Quaternary zonation of vegetation in the eastern Grand Canyon. Science 217:1142–1145.

COLE, K. L., AND L. MAYER. 1982. Use of packrat middens to determine rates of cliff retreat in the eastern Grand Canyon, Arizona. Geology 10:597–599.

COTTAM, W. P., J. M. TUCKER, AND R. DROBNIK. 1959. Some clues to Great Basin postpluvial climates provided by oak distributions. Ecology 40:362–377.

CRITCHFIELD, W. B. 1980. Genetics of lodgepole pine. USDA For. Ser. Res. Pap. WO-37, 57 pp.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora I. Hafner Publishing Co., New York and London. 270 pp.

DAUBENMIRE, R. 1943. Vegetational zonation in the Rocky Mountains. Bot. Rev. 9:325–393.

DAVIS, M. B. 1963. On the theory of pollen analysis. Amer. J. Sci. 261:897–911.

DAVIS, M. G., L. W. SPEAR, AND L. C. K. SHANE. 1980. Holocene climate of New England. Quat. Res. 14:240–250.

DEBUCHANANNE, G. D. 1974. Geohydrologic considerations in the management of radioactive waste. Nucl. Tech. 24:354–361.

DURRELL, L. W. 1916. Notes on some North American conifers based on leaf clusters. Proc. Iowa Acad. Sci. 23:519–582.

ELLISON, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecol. Monog. 24:89–184.

EPSTEIN, S., P. THOMPSON, AND C. J. YAPP. 1977. Oxygen and hydrogen isotopic ratios in plant cellulose. Science 198:1209–1215.

FOWELLS, H. A., AND B. M. KIRK. 1945. Availability of soil moisture to ponderosa pine. J. For. 43:601–604.

GALLOWAY, R. W. 1970. The full-glacial in the southwestern United States. Ann. Assoc. Amer. Geog. 60:245–256.

GIFFORD, R. O., G. L. ASHEROFT, AND D. MAGNOSON. 1967. Probability of selected precipitation amounts in the western region of the United States. Utah Agric. Expt. Sta. Mim. Ser. No. 500.

GREGORY, H. E. 1938. The San Juan County: a geographic and geologic reconnaissance of southeastern Utah. U.S. Geol. Sur. Prof. Pap. 188. 123 pp.

HALES, J. E., JR. 1974. Southwestern United States summer monsoon source—Gulf of Mexico or Pacific Ocean? J. Appl. Meteor. 13:331–342.

HARING, I. M. 1961. A checklist of the mosses of the state of Arizona. Bryologist 64:222–240.

HARLOW, W. M. 1931. The identification of the pines of the United States, native and introduced, by needle structure. New York State Col. For. at Syracuse Univ. Tech. Pub. 32 (Bull. Vol. 20, No. 2): 19 pp.

HEWITT, N. J. 1980. The occurrence of pinyon pine at Cowboy Cave. Univ. Utah Anthr. Pap. 104:163–177.

HOUGHTON, J. G. 1979. A model for orographic precipitation in the north central Great Basin. Month. Weath. Rev. 107:1462–1475.

KLEIN, J., J. C. LERMAN, P. E. DAMON, AND E. K. RALPH. 1982. Calibration of radiocarbon dates: tables based on the consensus data of the workshop on calibrating the radiocarbon time scale. Radiocarbon 24:103–150.

KUTZBACH, J. E. 1981. Monsoon climate of the early Holocene—climate experiment with the Earth's orbital parameters for 9000 years ago. Science 214:59–61.

KUTZBACH, J. E., AND R. L. OTTO-BLIESNER. 1982. The sensitivity of the African-Asian monsoonal climate to orbital parameter changes for 9000 yr. B.P. in a low-resolution general circulation model. J. Atmos. Sci. 39:1177–1188.

Lanner, R. M. 1974. Natural hybridization between *Pinus edulis* and *Pinus monophylla* in the American Southwest. Silv. Gen. 23:108–115.

Lull, H. W., and L. Ellison. 1950. Precipitation in relation to altitude in central Utah. Ecology 31:479–484.

Maher, L. J., Jr. 1963. Pollen analysis of surface materials from the southern San Juan Mountains, Colorado. Geol. Soc. Amer. Bull. 74:1485–1503.

Martin, P. S. 1963. The last 10,000 years: a fossil pollen record of the American Southwest. Univ. of Arizona Press. 87 pp.

Mead, J. I. 1981. The last 30,000 years of faunal history within the Grand Canyon, Arizona. Quat. Res. 15:311–326.

——. 1983. Harrington's extinct mountain goat (*Oreamnos harringtoni*) and its environment in the Grand Canyon. Unpublished dissertation, Univ. of Arizona, Tucson. 215 pp.

Mead, J. I., and A. M. Phillips, III. 1981. The late Pleistocene and Holocene fauna and flora of Vulture Cave, Grand Canyon, Arizona. Southw. Nat. 26:257–288.

Mead, J. I., R. S. Thompson, and A. Long. 1978. Arizona radiocarbon dates 9: Carbon isotope dating of packrat middens. Radiocarbon 20:171–191.

Mitchell, V. L. 1976. The regionalization of climate in the western United States. J. Appl. Meteor. 15:920–927.

Miles, M. K. 1978. Predicting temperature trends in the Northern Hemisphere to the year 2000. Nature 276:356–359.

Mullen, S. L. 1979. An investigation of small synoptic scale cyclones in polar air streams. Month. Weath. Rev. 107:1636–1647.

Neilson, R. P., and L. H. Wullstein. 1983. Biogeography of two southwest American oaks in relation to atmospheric dynamics. J. Biogeog. 10:275–297.

Pearson, G. A. 1950. Management of ponderosa pine in the southwest. USDA Agric. Monog. 6: 218 pp.

Peet, R. K. 1978. Forest vegetation of the Colorado Front Range: patterns of species diversity. Vegetatio 37:65–78.

Phillips, A. M., III. 1977. Packrats, plants and the Pleistocene in the lower Grand Canyon. Unpublished dissertation. Univ. of Arizona, Tucson. 123 pp.

Price, R., and R. B. Evans. 1937. Climate of the west front of the Wasatch Plateau in central Utah. Month. Weath. Rev. 65:291–301.

Prudden, T. M. 1903. The prehistoric ruins of the San Juan watershed in Utah, Arizona, Colorado and New Mexico. Amer. Anthr. 5:224–228.

Raun, G. G. 1966. A population of woodrats (*Neotoma micropus*) in southern Texas. Texas Mem. Mus. Bull. 11.

Reed, R. J. 1979. Cyclogenesis in polar air streams. Month. Weath. Rev. 107:38–52.

Reveal, J. L. 1979. Biogeography of the Intermountain region: a speculative appraisal. Mentzelia 4.

Richmond, G. M. 1962. Quaternary stratigraphy of the La Sal Mountains, Utah. U.S. Geol. Surv. Prof. Pap. 324.

Sellers, W. D. 1960. Precipitation in Arizona and western New Mexico. Pages 81–94 *in* Proc. 28th Annual Meet., Western Snow Conference, Santa Fe.

Siegel, R. D. 1983. Paleoclimatic significance of D/H and $^{13}C/^{12}C$ ratios in Pleistocene and Holocene wood. Unpublished thesis, Univ. of Arizona, Tucson. 105 pp.

Spaulding, W. G. 1981. The late Quaternary vegetation of southern Nevada mountain range. Unpublished dissertation. Univ. of Arizona, Tucson. 271 pp.

——. In press. Vegetation and climates of the last 45,000 years at the Nevada Test Site and vicinity. U.S. Geol. Prof. Pap.

Spaulding, W. G., and K. L. Petersen. 1980. Late Pleistocene and early Holocene paleoecology of Cowboy Cave. Univ. Utah Anthr. Pap. 104:163–177.

Spaulding, W. G., E. P. Leopold, and T. R. Van Devender. 1983. Late Wisconsin paleoecology of the American Southwest. *In* S. C. Porter, The Late Pleistocene of the United States: a review. Univ. of Minnesota Press, Minneapolis. 407 pp.

Steinhoff, R. J., and J. W. Andersen. 1971. Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silv. Gen. 20:159–167.

Stones, R. C., and C. L. Hayward. 1968. Natural history of the desert woodrat, *Neotoma lepida*. Amer. Midl. Nat. 80(2):458–476.

Thompson, R. S., and E. M. Hattori. 1983. Packrat (Neotoma) middens from Gatecliff Shelter and Holocene migration of woodland plants. *In* D. H. Thomas, The archaeology of Monitor Valley 2, Gatecliff Shelter. Amer. Mus. Nat. Hist. Anthr. Pap. 59:157–167.

Thompson, R. S., and J. I. Mead. 1982. Late Quaternary environments and biogeography in the Great Basin. Quat. Res. 17:39–55.

Thompson, R. S., and T. R. Van Devender. 1982. Late Pleistocene vegetational records from desert grassland in the Santa Catalina Mountains, Arizona. Amer. Quat. Assoc. Abs. 7:167.

Van Devender, T. R. 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southwestern Arizona. Unpublished dissertation. Univ. of Arizona, Tucson. 179 pp.

Van Devender, T. R., J. L. Betancourt, and M. Wimberly. *In* press. Biogeographic implications of a packrat midden sequence from the Sacramento Mountains, southern New Mexico. Quat. Res.

Van Devender, T. R., and J. I. Mead. 1976. Late Pleistocene and modern plant communities of Shinumo Creek and Peach Springs Wash, Lower Grand Canyon, Arizona. J. Ariz. Nev. Acad. Sci. 11:16–22.

Van Devender, T. R., and W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701–710.

Vasek, F. C. 1966. The distribution and taxonomy of three western junipers. Brittonia 18:350–372.

WELLS, P. V. 1976. Macrofossil analysis of woodrat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. Quat. Res. 6:223–248.

______. 1979. An equable glacio-pluvial in the West: periglacial evidence of increased precipitation on a gradient from the Great Basin to the Sonoran and Chihuahuan deserts. Quat. Res. 12:311–325.

WELSH, S. L. 1978. Problems in plant endemism on the Colorado Plateau. Great Basin Nat. Mem. 2:191–195.

WILLIAMS, P., JR., AND E. L. PECK. 1962. Terrain influences on precipitation in the Intermountain West as related to synoptic situations. J. Appl. Meteor. 1:343–347.

WITKIND, I. J. 1965. Geology of the Abajo Mountains area, San Juan County, Utah. U.S. Geol. Prof. Pap. 435.

WRIGHT, H. E., JR., A. M. BENT, B. S. HANSEN, AND L. J. MAHER, JR. 1973. Present and past vegetation of the Chuska Mountains, northwestern New Mexico. Geol. Soc. Am. Bull. 84:1155–1180.

DIATOMS IN RECENT BOTTOM SEDIMENTS AND TROPHIC STATUS OF EIGHT LAKES AND RESERVOIRS IN NORTHEASTERN UTAH

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Abstract.— Recent bottom sediments of eight lakes and reservoirs in northeastern Utah were examined. One hundred and sixty-four diatom taxa were identified and their relative abundances determined. Seven stand associations were evident by cluster analysis of similarity indices. These association patterns mirrored trophic status of the waters. Shannon-Wiener species diversity values were also determined. The diversities fell in patterns that were similar to the stand associations determined by cluster analysis. The most prevalent diatom taxa encountered in this study were found mostly in eutrophic waters. These taxa included *Stephanodiscus astraea*, *Stephanodiscus astraea* var. *minutula*, *Asterionella formosa*, and *Fragilaria crotonensis*. A wide variety of other taxa dominated various mesotrophic and oligotrophic sites.

A large literature on paleodiatomological investigations is extant, but few publications deal with diatoms in recent sediments (Kaczmarska 1976). Stockner and Benson (1967) examined diatom succession in recent sediments of Lake Washington. Stockner (1971) developed a classification scheme for deep water lakes, based on the A/C ratio (A = Araphidinae; C = Centrales) of diatoms in recent bottom sediments and plankton. Nevertheless, he commented that his scheme did not adequately characterize the current trophic state of shallow isothermal lakes or man-made reservoirs (Stockner 1972). Duthie and Sreenivasa (1972) studied the horizontal distribution of diatoms in recent sediments of Lake Ontario and attempted to correlate the results with chemical and other environmental factors. They also examined the relationship between the sedimentary diatom flora and the planktonic flora. Bortleson and Lee (1975) looked for evidence of cultural eutrophication from recent sediment layers in lakes. This study was more concerned with pronounced changes in chemical stratigraphy than diatom deposition and floristics.

Biological systems are most sensitive to the effects of pollution on the environment; yet, until recent years, biological studies have played a minor role in water quality assessment. Diatoms have been especially neglected in these studies. Cairns and Dickson (1971) have listed several factors contributing to this neglect. In the last 10 years, however, diatoms have been studied more thoroughly with respect to water quality and have graduated to a position of importance.

For several years in our laboratory we have pursued studies of the use of diatoms to assess water quality and trophic status of lakes, reservoirs, and streams throughout the intermountain west of North America (Merritt et al. 1977a, 1977b). Through such work, we have come to believe that diatom assemblages found in recent bottom sediments offer an attractive and important index of lake and reservoir ecology. The objectives of the present study were: (1) to determine the diatom species present in recent bottom sediments in several lakes and reservoirs in Utah, (2) to determine if diatoms found in the bottom sediments reflect the trophic status of such waters, and (3) to attempt to determine which species or groups of species are indicators of trophic status by using statistical analyses to correlate with known chemical and physical parameters associated with the lakes.

Site Descriptions

Eight lakes and reservoirs were selected for study. These lakes were selected for analysis as part of Environmental Protection Agency Program 208 Areawide Water Quality Studies. Research reports of these studies classified these lakes as oligotrophic, mesotrophic, and eutrophic (Environmental Protection Agency 1976, Merritt et al. 1977a, 1977b). The trophic status of each lake and reservoir was determined by assessing all environmental data available, including floristics, standing crop, water chemistry, etc. Table 1 summarizes lake or reservoir morphometry. The following site descriptions briefly characterize each lake or reservoir studied (Fig. 1). More detailed descriptions can be found in Merritt et al. (1977a, 1977b).

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Steinaker Reservoir

Steinaker Reservoir is on Steinaker Draw, a tributary of Ashley Creek approximately 6 km north of Vernal, Uintah County, in eastern Utah. It has been classified as an oligo-mesotrophic system, tending more toward mesotrophy. The reservoir is relatively shallow, with a mean depth of 14.2 m and is fairly productive. Seasonal patterns and demand for irrigation water produce a widely fluctuating water level. The shallow depth results in a fairly large littoral zone. Bottom sediments were collected from two sites (Merritt et al. 1977b).

Starvation Reservoir

Starvation Reservoir is in northeastern Utah in Duchesne County on the Strawberry River, which is a tributary of the Duchesne River. Duchesne township is approximately 5 km southwest of the lake. Merritt et al. (1977b) classified this lake as a mesotrophic system. Their data suggest that the reservoir is maintaining its mesotrophic condition. Starvation Reservoir fluctuates widely in depth due to utilization of its water for irrigation. Samples were collected from two sites (Merritt et al. 1977b).

Moon Lake

Moon Lake is situated near Mountain Home, Duchesne County, Utah, and is fed by the Lakefork River. This lake is a high-mountain oligotrophic system. The lake is used for irrigation and recreation. Bottom sediments were collected from one site near the dam (Merritt et al. 1977b).

Strawberry Reservoir

Strawberry Reservoir is located on the Strawberry River in Wasatch County, Utah. It is situated in a valley east of the Wasatch Range and is approximately 40 km due east of Provo. Next to Utah Lake, this is the largest body of water in this study. This reservoir has always been a highly productive system, which is reflected in its classification as eutrophic with definite anoxic conditions below 6 m. It is older than the other reservoirs in our study. The deeper regions of the lake exceed 18 m, although overall it is fairly shallow, averaging about 9 m. Nineteen samples were collected from all parts of the lake

TABLE 1. Summary of morphometric data of lakes and reservoirs examined during this study.

	Strawberry Reservoir	Deer Creek Reservoir	Rockport Reservoir	Steinaker Reservoir	Starvation Reservoir	Echo Reservoir	Utah Lake	Moon Lake
Surface area (km^2)	34.2	11.3	4.8	3.3	13.4	5.9	385.1	3.1
Volume (x10^{6}m^3)	357.8	193.9	93.4	47.1	206.4	91.2	1108.0	44.1
Mean depth (m)	10.5	18.4	19.4	14.2	15.4	15.5	2.9	14.2
Maximum depth (m)	18.6	41.8	45.7	42.1	44.8	33.5	4.3	20.1
Spillway elevation (m)	2303	1651	1843	1677	1683	1694	1368	2470
Mean annual precipitation (cm)	54	54	40	20	19	36	46	43
Drainage area (km^2)	440	1450	828	54	1554	2745	6876	276
[*]Mean hydraulic retention time (yrs)	4.5	0.6	0.6	2.0	1.9	0.4	2.5	0.4

[*] Based on outflow.

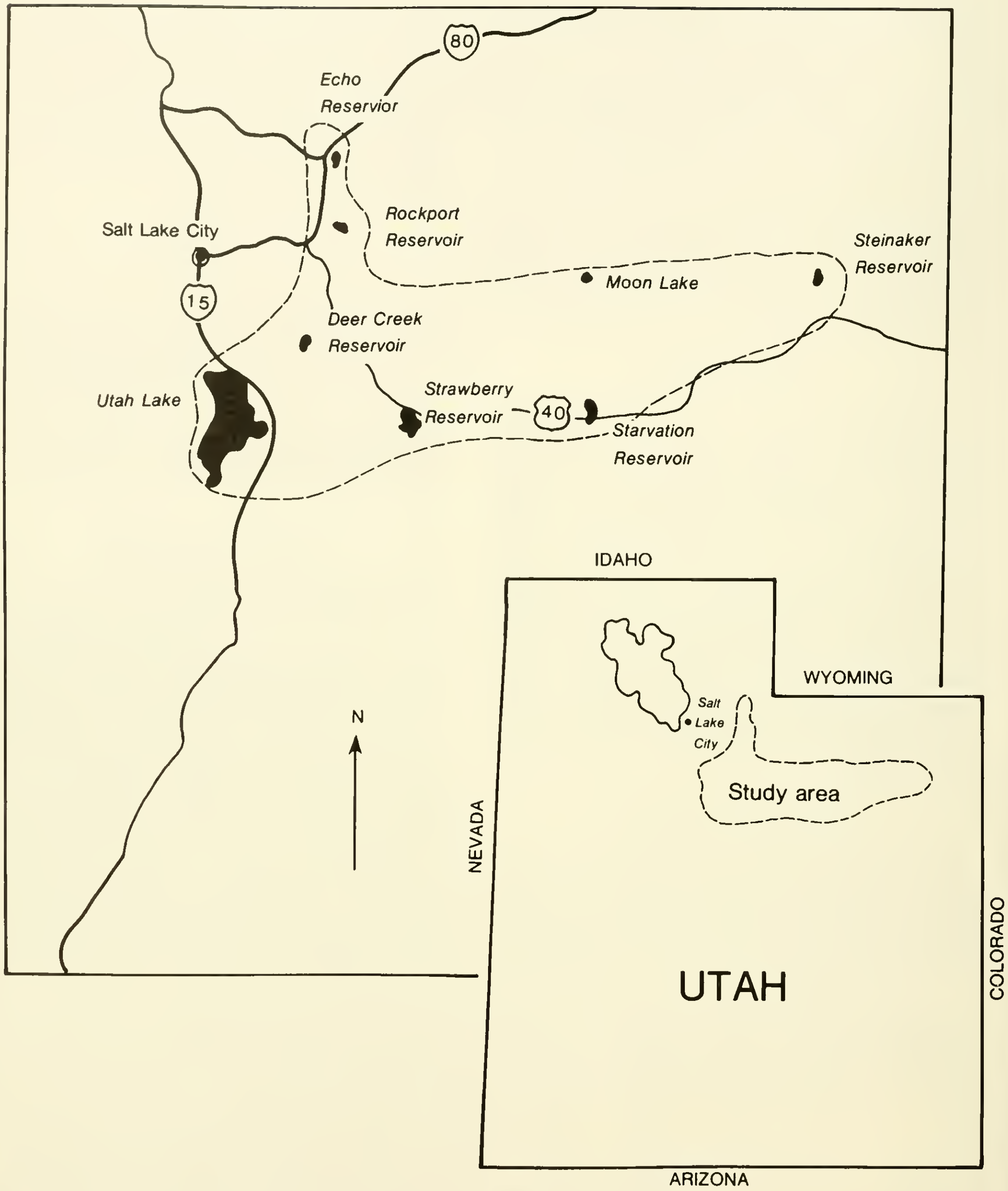
80
Echo
Reservior
Rockport
Reservoir
Salt Lake City
15
Steinaker
Reservoir
Moon Lake
Deer Creek
Reservoir
Utah Lake
Strawberry
Reservoir
40
Starvation
Reservoir
N
IDAHO
WYOMING
Salt
Lake
City
Study area
NEVADA
UTAH
COLORADO
ARIZONA

Fig. 1. Map of Utah showing the location of the lakes and reservoirs in the study area.

(Mountainland Association of Governments 1977a, 1977b).

Echo Reservoir

Echo Reservoir was formed on the Weber River in Summit County, Utah, immediately north of the town of Coalville. This reservoir is presently classified as eutrophic by Merritt et al. (1977a). Recent algal productivity figures indicate that the lake is mesotrophic even though other parameters indicate eutrophy (Merritt et al. 1977a). Similar to most of the lakes considered in our study, Echo Reservoir is subject to a heavy drawdown in dry years as a result of irrigation. Six sites were selected for collections (Mountainland Association of Governments 1977a, 1977b).

Rockport Reservoir

Rockport Reservoir was formed by damming the Weber River, Summit County, Utah, approximately 15 km upstream (southeast) from Echo Reservoir. The town of Peoa is about 8 km south of the lake, and Wanship is about 3 km north of the dam. This reservoir is not subjected to as heavy a drawdown as Echo Reservoir, although it is also used for storage of irrigation water. There is also a small municipal demand for this water. The reservoir was classified as mesotrophic to eutrophic. Five collection sites were established on Rockport Reservoir (Mountainland Association of Governments 1977a, 1977b).

Deer Creek Reservoir

Deer Creek Reservoir is on the Provo River approximately 7 km southwest of the town of Heber in north central Utah in Wasatch County. Not only is it a major water storage site for irrigation, but it also supplies culinary water for several municipalities. The north part of the lake is shallow and eutrophic, and the south part of the lake is deeper, with a lower standing crop, and meso-eutrophic in nature (Merritt et al. 1977a). Ten collection sites were established (Mountainland Association of Governments 1977a, 1977b).

Utah Lake

Utah Lake is at the mouth of the Provo River in an intermountain basin, bounded on the west by Lake Mountain and on the east by the Wasatch Mountains (Bolland 1974). It is the largest freshwater lake in Utah and is a natural reservoir. With increasing population, it has become a site for dumping industrial, municipal, and agricultural waste waters. This lake has been classified both as a highly eutrophic freshwater lake and as a moderately saline desert or prairie lake. Samples of recent bottom sediments were collected by following the transects established by Whiting et al. (1978). Eight collection sites were established (Mountainland Association of Governments 1977a, 1977b).

METHODS

Field and Laboratory

Samples were collected from recent bottom sediments using an Eckmann dredge sampler. Collections were made between May and August of 1975 except for two samples collected in February 1976. Sediment samples were transferred to 250 ml plastic jars and returned to the laboratory for processing. Permanent diatom slides were prepared following standard nitric acid oxidation methods (St. Clair and Rushforth 1977) and were mounted in Naphrax diatom mountant. Slides were examined and diatom species identified under 1000 X with Ziess RA microscopes.

Data Analyses

Quantitative data on the diatom species were recorded by counting approximately 400 diatoms from each sample. These results were converted into percent relative density values for all species for each site. Shannon-Wiener diversity indices were calculated for individual samples (Margalef 1958).

Similarity indices were computed from relative density data for each stand relative to all other stands (Ruzicka 1958). Stand cluster analyses (Sneath and Sokal 1973) from similarity indices were performed to identify if and where unique communities occurred within and between each individual lake and reservoir. This clustering technique computes the average similarity of each stand to each other stand using arithmetic averages. It has been found to introduce less distortion than other methods (Kaesler and Cairns 1972). Lakes were also clustered to identify possible unique lake associations. This was done by averaging percent relative density for each species in all stands of each lake or reservoir and comparing the degree of similarity between any two waters. Cluster patterns among our reservoirs and lakes with known trophic states were used to determine if the diatoms in the recent bottom sediments significantly differ in lakes of different trophic states.

The most important diatoms in the study as a whole and the diatoms most important in stand clusters were determined using an importance index. This index was calculated by multiplying frequency times percent relative density (Warner and Harper 1972). Distribution of important diatoms along trophic level gradients was evaluated to determine broadly niched, tolerant species and restricted species.

Results and Discussion

One hundred and sixty-four diatom taxa were identified and their occurrence and relative density in 53 samples were noted. The most abundant organisms were planktonic species of *Stephanodiscus*, *Fragilaria*, *Melosira*, and *Asterionella*. Still, over 90 percent of all species were nonplanktonic diatoms. Table 2 contains a phylogenetic list of all diatoms identified.

Diatoms were ranked by importance values (Warner and Harper 1972) for all stands as well as for each lake and reservoir (Table 3). The most prevalent diatom taxa in this study were *Stephanodiscus astraea*, *Stephanodiscus astraea* var. *minutula*, *Asterionella formosa*, *Fragilaria crotonensis*, and *Stephanodiscus niagarae.* In addition, the following diatoms were locally important: *Achnanthes minutissima* was common in the mesotrophic, saline-eutrophic, and oligotrophic systems, and *Melosira granulata* was common in the mesotrophic and mildly eutrophic samples. *Diatoma vulgare* and *Cymbella affinis* were dominant in certain local areas of Rockport Reservoir and certain sites in Utah Lake. *Epithemia sorex* and *Cyclotella bodanica* were common in Steinaker Reservoir but were otherwise restricted in importance. Utah Lake was dominated by *Stephanodiscus astraea* var. *minutula* and *Melosira granulata* var. *angustissima*, and contained significant numbers of *Cyclotella meneghiniana. Nitzschia palea* and *Navicula cryptocephala* var. *veneta* were found commonly in the study area but were highest in occurrence in Moon Lake. *Achnanthes lanceolata* var. *dubia*, *Navicula cryptocephala*, *Navicula pupula*, and *Caloneis bacillum* were also common only in Moon Lake.

The results of our lake and reservoir cluster are presented in a dendrogram (Fig. 2).

Table 2. Phylogenetic list of diatom taxa found in recent bottom sediments of the selected lakes and reservoirs examined during this study.

Coscinodiscaceae
Cyclotella bodanica Eulenst.
Cyclotella kutzingiana Thwaites
Cyclotella meneghiniana Kutzing
Cyclotella ocellata Pantocsek
Melosira granulata (Ehr.) Ralfs
Melosira granulata var. *angustissima* Mueller
Melosira varians Agardh
Stephanodiscus astraea (Ehr.) Grunow
Stephanodiscus astraea var. *minutula* (Kutz.) Grunow
Stephanodiscus niagarae Ehrenberg

Fragilariaceae
Asterionella formosa Hassall
Diatoma anceps (Ehr.) Kirchner
Diatoma hiemale var. *mesodon* (Ehr.) Grunow
Diatoma tenue var. *elongatum* Lyngbye
Diatoma vulgare Bory
Diatoma vulgare var. *grande* (W.Sm.) Grunow
Fragilaria brevistriata Grunow
Fragilaria brevistriata var. *inflata* (Pant.) Hustedt
Fragilaria capucina var. *mesolepta* Rabenhorst
Fragilaria construens (Ehr.) Grunow
Fragilaria construens var. *binodis* (Ehr.) Grunow
Fragilaria construens var. *venter* (Ehr.) Grunow
Fragilaria crotonensis Kitton
Fragilaria leptostauron (Ehr.) Hustedt
Fragilaria leptostauron var. *dubia* (Grun.) Hustedt
Fragilaria pinnata var. *lancettula* (Schum.) Hustedt
Fragilaria vaucheriae (Kutz.) Petersen
Hannaea arcus (Ehr.) Patrick
Meridion circulare (Gr.) Agardh
Opephora martyi Heribaud
Synedra acus Kutzing
Synedra amphicephala Kutzing
Synedra capitata Ehrenberg
Synedra cyclopum Brutschy
Synedra cyclopum var. *robustum* Schultz
Synedra delicatissima W. Smith
Synedra parasitica var. *subconstricta* (Grun.) Hustedt
Synedra rumpens Kutzing
Synedra rumpens var. *fragilariodes* Grunow
Synedra socia Wallace
Synedra ulna (Nitz.) Ehrenberg
Synedra ulna var. *contracta* Oestrup
Tabellaria flocculosa (Roth) Kutzing

Eunotiaceae
Eunotia arcus var. *bidens* Grunow

Achnanthaceae
Achnanthes exigua Grunow
Achnanthes hungarica Grunow
Achnanthes lanceolata (Breb.) Grunow
Achnanthes lanceolata var. *dubia* Grunow
Achnanthes linearis (W.Sm.) Grunow
Achnanthes minutissima Kutzing
Cocconeis disculus Schumann
Cocconeis pediculus Ehrenberg
Cocconeis placentula Ehrenberg

Table 2 continued.

Cocconeis placentula var. *euglypta* (Ehr.) Cleve
Cocconeis placentula var. *lineata* (Ehr.) v. Heurck
Rhoicosphenia curvata (Kutz.) Grunow

NAVICULACEAE
Caloneis amphisbaena (Bory) Cleve
Caloneis bacillum (Grun.) Cleve
Caloneis fenzlii (Grun.) Patrick
Caloneis lewisii Patrick
Diploneis elliptica (Kutz.) Cleve
Diploneis smithii (Breb.) Cleve
Frustulia vulgaris Thwaites
Gyrosigma acuminatum Kutzing
Gyrosigma macrum (W.Sm.) Griff. and Henfr.
Navicula anglica Grunow
Navicula arvensis Hustedt
Navicula bacillum Ehrenberg
Navicula bicephala Hustedt
Navicula capitata Ehrenberg
Navicula capitata var. *hungarica* (Grun.) Ross
Navicula circumtexta Meist. ex Hustedt
Navicula cryptocephala Kutzing
Navicula cryptocephala var. *veneta* (Kutz.) Rabenhorst
Navicula cuspidata (Kutz.) Kutzing
Navicula exigua var. *capitata* Patrick
Navicula graciloides A. Mayer
Navicula gysingensis Foged
Navicula lanceolata (Ag.) Kutzing
Navicula laterostrata Hustedt
Navicula minima Grunow
Navicula oblonga (Kutz.) Kutzing
Navicula pelliculosa (Breb. ex Kutz.) Hilse
Navicula pseudoreinhardtii Patrick
Navicula pupula Kutzing
Navicula pupula var. *rectangularis* (Greg.) Grunow
Navicula pygmaea Kutzing
Navicula radiosa Kutzing
Navicula radiosa var. *tenella* (Breb. ex Kutz.) Grunow
Navicula reinhardtii (Grun.) Grunow
Navicula rhyncocephala Kutzing
Navicula salinarum Grunow
Navicula salinarum var. *intermedia* (Grun.) Cleve
Navicula secreta Krasske
Navicula seminulum Grunow
Navicula tripunctata (O. Muel.) Bory
Navicula variostriata Krasske
Navicula viridula Kutz. em v. Heurck
Navicula viridula var. *avenacea* (Breb. ex Grun.) v. Heurck
Neidium binode (Ehr.) Hustedt
Neidium dubium (Ehr.) Cleve
Neidium iridis (Ehr.) Cleve
Pinnularia biceps Gregory
Pinnularia brebissonii Kutzing
Pinnularia viridis (Nitz.) Ehrenberg
Pinnularia viridis var. *minor* Cleve
Pleurosigma australe Grunow
Pleurosigma delicatulum W. Smith
Stauroneis anceps Ehrenberg
Stauroneis anceps var. *gracillis* Rabenhorst
Stauroneis anceps var. *linearis* (Ehr.) Cleve
Stauroneis phoenicenteron Ehrenberg
Stauroneis smithii var. *incisa* Pantocsek

Table 2 continued.

CYMBELLACEAE
Amphora ovalis Kutzing
Amphora ovalis var. *pediculus* Kutzing
Amphora perpusilla Grunow
Amphora veneta Kutzing
Cymbella affinis Kutzing
Cymbella cistula (Hemp.) Grunow
Cymbella delicatula Kutzing
Cymbella gracilis (Rabh.) Cleve
Cymbella mexicana (Ehr.) Cleve
Cymbella microcephala Grunow
Cymbella prostrata (Berk.) Cleve
Cymbella sinuata Gregory
Cymbella ventricosa Kutzing

GOMPHONEMACEAE
Gomphoneis herculeana (Ehr.) Cleve
Gomphonema acuminatum Ehrenberg
Gomphonema angustatum (Kutz.) Rabenhorst
Gomphonema constrictum Ehrenberg
Gomphonema gracile Ehrenberg
Gomphonema intricatum Kutzing
Gomphonema intricatum var. *pumila* Grunow
Gomphonema olivaceum (Lyng.) Kutzing
Gomphonema parvulum Kutzing

EPITHEMIACEAE
Denticula elegans Kutzing
Epithemia argus Kutzing
Epithemia sorex Kutzing
Epithemia turgida (Ehr.) Kutzing
Epithemia adnata (Kutz.) Brebisson
Rhopalodia gibba (Ehr.) O. Mueller
Rhopalodia gibba var. *ventricosa* (Kutz.) Peragallo
Rhopalodia gibberula (Ehr.) O. Mueller

NITZSCHIACEAE
Bacillaria paradoxa Gmelin
Hantzschia amphioxys (Ehr.) Grunow
Nitzschia amphibia Grunow
Nitzschia angustata (W.Sm.) Grunow
Nitzschia dissipata (Kutz.) Grunow
Nitzschia fonticola Grunow
Nitzschia frustulum Kutzing
Nitzschia hungarica Grunow
Nitzschia linearis W. Smith
Nitzschia palea (Kutz.) W. Smith
Nitzschia punctata (W.Sm.) Grunow
Nitzschia sigmoidea (Ehr.) W. Smith
Nitzschia tryblionella var. *levidensis* Hantzsch
Nitzschia species

SURIBELLACEAE
Cymatopleura elliptica (Breb.) W. Smith
Cymatopleura solea (Breb.) W. Smith
Surirella angustata Kutzing
Surirella ovalis Brebisson
Surirella ovata Kutzing
Surirella robusta Ehrenberg
Surirella spiralis Kutzing

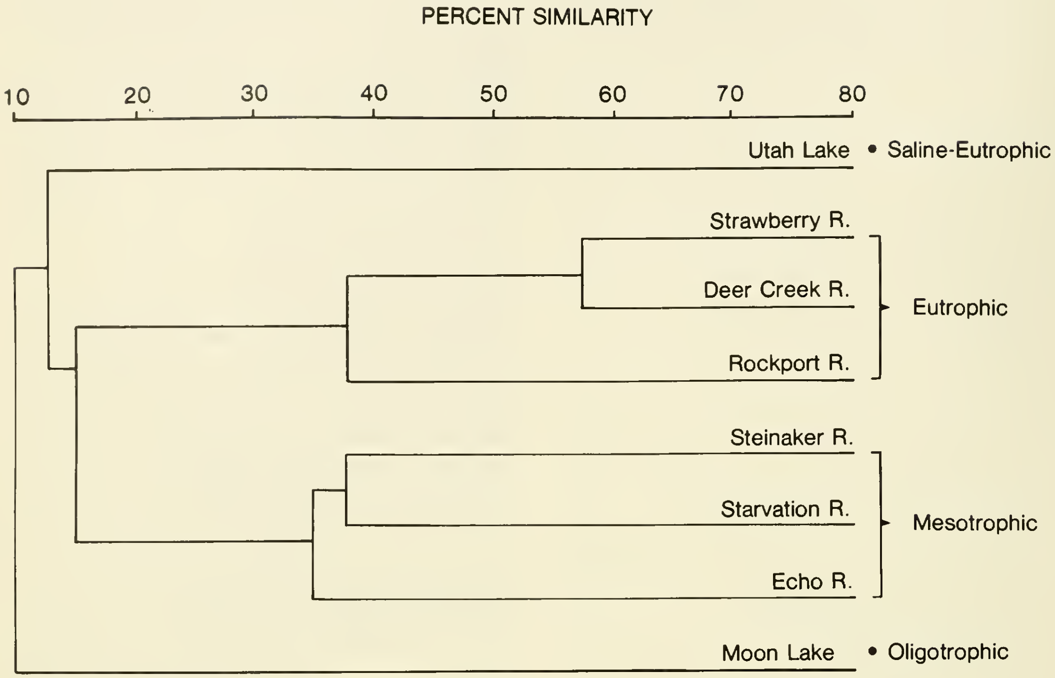

Fig. 2. Cluster dendrogram showing similarities between stands from different lakes and reservoirs.

The cluster pattern supported previous evidence for the general trophic status of each lake and reservoir (Merritt et al. 1977a, 1977b). The eutrophic Strawberry and Deer Creek reservoirs clustered fairly tightly, with 58% similarity. Rockport Reservoir, a meso-eutrophic system, clustered with these two but at a lower level of similarity (38%). The mesotrophic Steinaker, Starvation, and Echo reservoirs clustered together fairly loosely at about 36% similarity. These reservoirs are at various levels of mesotrophy and each has a potential for rapid eutrophy. Utah Lake is a large, slightly saline eutrophic lake with little similarity to the other waters studied. The same is true for the oligotrophic Moon Lake.

The results of clustering our 53 stands are presented in Figure 3. Four major clusters and seven subgroups are evident in this dendrogram. The cluster pattern, based on species occurring in each stand, yielded groups representative of various degrees of eutrophication. In addition, species diversity of diatom populations, as measured by the Shannon-Wiener index, correlated with the trophic status of the collection sites (Fig. 4). The majority of our stands reflect the current view that oligotrophic or somewhat mesotrophic waters tend to support highly diverse floras, and more eutrophic waters support less diverse floras. For example, some samples from highly eutrophic sites with a very low species diversity contained only a few tolerant species. These samples tended to be highly similar and cluster tightly (Fig. 3). Certain stands in Strawberry Reservoir consisted of only four to six species with Shannon-Wiener diversity values of only 0.37 to 0.93 (Fig. 4). Such stands were as much as 89% similar. Other stands in the study area showed the opposite extreme. They had high species diversity, with as many as 60 species per stand. This produced Shannon-Wiener values above 3.0. Such stands occurred in oligotrophic sites. It is interesting that these oligotrophic stands showed much less similarity to one another (less than 28%) than the eutrophic stands.

Subgroup I (Fig. 3) is composed of stands from eutrophic sites. It is composed mostly of stands from Strawberry Reservoir, together with two Deer Creek Reservoir and three Rockport Reservoir stands. *Stephanodiscus astraea* dominated all sites. Over 85% of the population of half of these sites resulted from this species alone, with its average abundance being 82.3% (Table 4). *Asterionella formosa, Hantzschia amphioxys, Melosira granulata,* and *Cocconeis placentula* var. *lineata* were common, each in a separate sample of this subgroup. Tightness of clusters and low species diversity set these 17 samples apart from the rest of the stands in the study. Environmental data show that these stands are the most eutrophic in the study.

Subgroup II (Fig. 3) is a discrete group of Deer Creek Reservoir samples. These sites are characterized by the dominance of *Stephanodiscus astraea* and *Asterionella formosa. Stephanodiscus niagarae* was also common in all sites except one where it was replaced by *Fragilaria crotonensis.* This group of Deer Creek samples represents sites from the southern part of the lake. Merritt et al. (1977a) divided Deer Creek into two environmental types, the northern half being eutrophic and the southern meso-eutrophic. The two samples from Deer Creek that clustered in subgroup I are from the northern half of the reservoir and follow the designated eutrophic state. The seven samples in subgroup II are moderately eutrophic.

Subgroup III (Fig. 3) is a discrete group of three samples from Strawberry Reservoir.

TABLE 3. Summary of prevalent species in the lakes and reservoirs examined during this study. Species with average relative densities above the 3% level were included.

	All lakes and reservoirs	Strawberry Reservoir	Deer Creek Reservoir	Rockport Reservoir	Steinaker Reservoir	Starvation Reservoir	Echo Reservoir	Utah Lake	Moon Lake
Stephanodiscus astraea	37.4	58.7	56.8	47.6			5.8	3.1	
Stephanodiscus astraea var. *minutula*	11.2	15.5			8.5	12.6	11.0	23.4	
Asterionella formosa	8.9	5.0	20.9		10.5	17.4	14.7		13.0
Fragilaria crotonensis	5.1		3.2		27.0	39.5	14.8		5.0
Stephanodiscus niagarae	4.1	4.4	5.9			9.3	3.6	4.1	
Cocconeis placentula var. *lineata*		3.7			3.5				
Melosira granulata			4.2			11.5	3.5		
Diatoma vulgare				10.1			3.2		
Achnanthes minutissima				5.7	4.0		5.1	6.5	5.0
Cymbella affinis				5.0					
Amphora venata				3.3					
Navicula cryptocephala var. *venata*				3.3			3.5		9.0
Nitzschia palea					3.5		4.5		11.0
Epithemia sorex					7.5				
Cyclotella bodanica					5.0				
Achnanthes lanceolata					4.5		3.6		
Surirella ovalis							5.0		
Gomphonema olivaceum							3.5		
Melosira granulata var. *angustissima*								17.9	
Cyclotella meneghiniana								9.7	
Amphora ovalis								4.5	
Pleurosigma delicatulm								3.3	
Amphora ovalis var. *pediculus*								3.2	
Achnanthes lanceolata var. *dubia*									8.0
Navicula cryptocephala									6.0
Navicula pupula									6.0
Calonies bacillum									5.0
Tabellaria flocculosa									4.0
Synedra amphicephala									4.0
Nitzschia frustulum									3.0
Nitzschia linearis									3.0

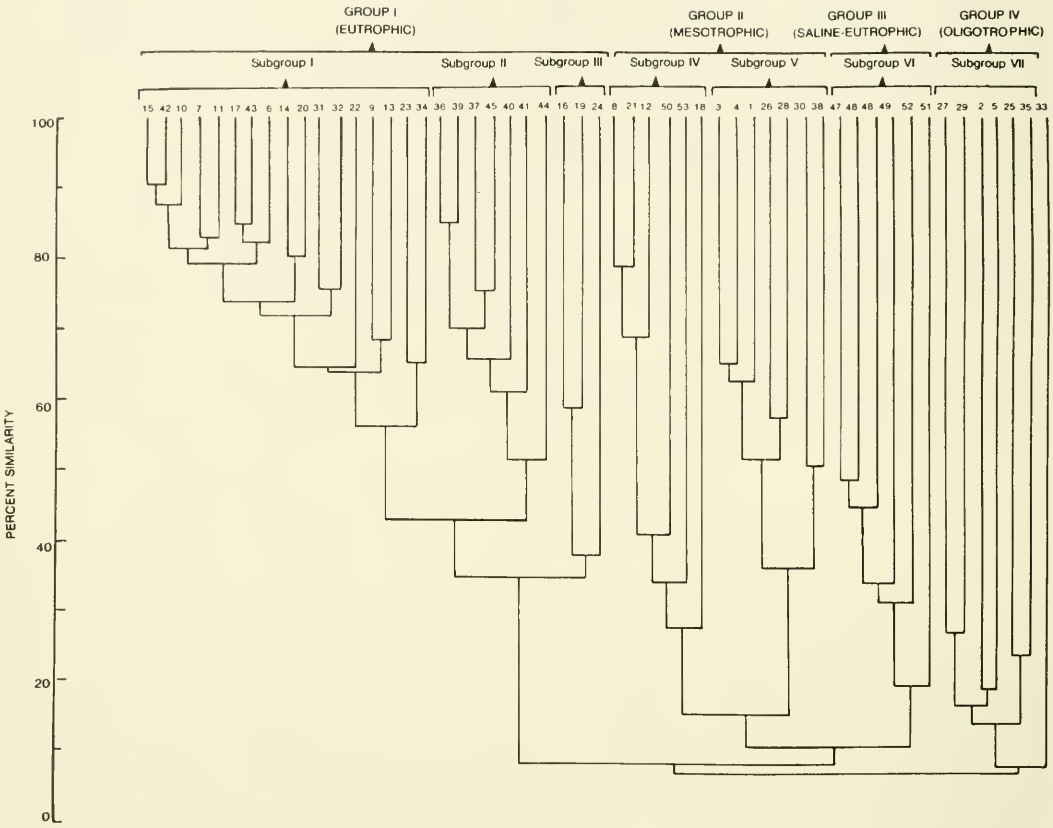

Fig. 3. Cluster dendrogram showing similarities of stands of diatoms in the study area. Sample numbers are shown within subgroups. An explanation of these numbers can be found in Table 5.

This unit is similar to Subgroup II. *Stephanodiscus astraea* is responsible for an average of 45% of the diatom populations. *Asterionella formosa* is replaced by *Cocconeis placentula* var. *lineata* in two of the samples and by *Nitzschia palea* and *Navicula lanceolata* in the third. These samples are probably meso-eutrophic stands in isolated parts of an otherwise highly eutrophic reservoir. For example, one of these samples was collected at the inlet of Strawberry River and would have a strong river influence that would isolate it from the surrounding reservoir type.

Subgroup IV (Fig. 3) is dominated by *Stephanodiscus astraea* var. *minutula*. Beyond this species, similarity between stands is relatively low. The subgroup is composed of three Strawberry Reservoir samples that are eutrophic and differ from subgroup I by having a variety of *Stephanodiscus astraea* as the dominant form. A fourth Strawberry Reservoir sample is uniquely dominated by *Stephanodiscus niagarae* and *Stephanodiscus astraea* var. *minutula*. The other two samples making up this subgroup were from Utah Lake. Their uniqueness is ascribed to the commonness of *Diatoma vulgare* in one sample and *Achnanthes minutissima* in the other. Both these samples differ strongly from the rest taken from Utah Lake. One was taken from Provo Bay, an isolated area with lower turbidity and TDS than the rest of the

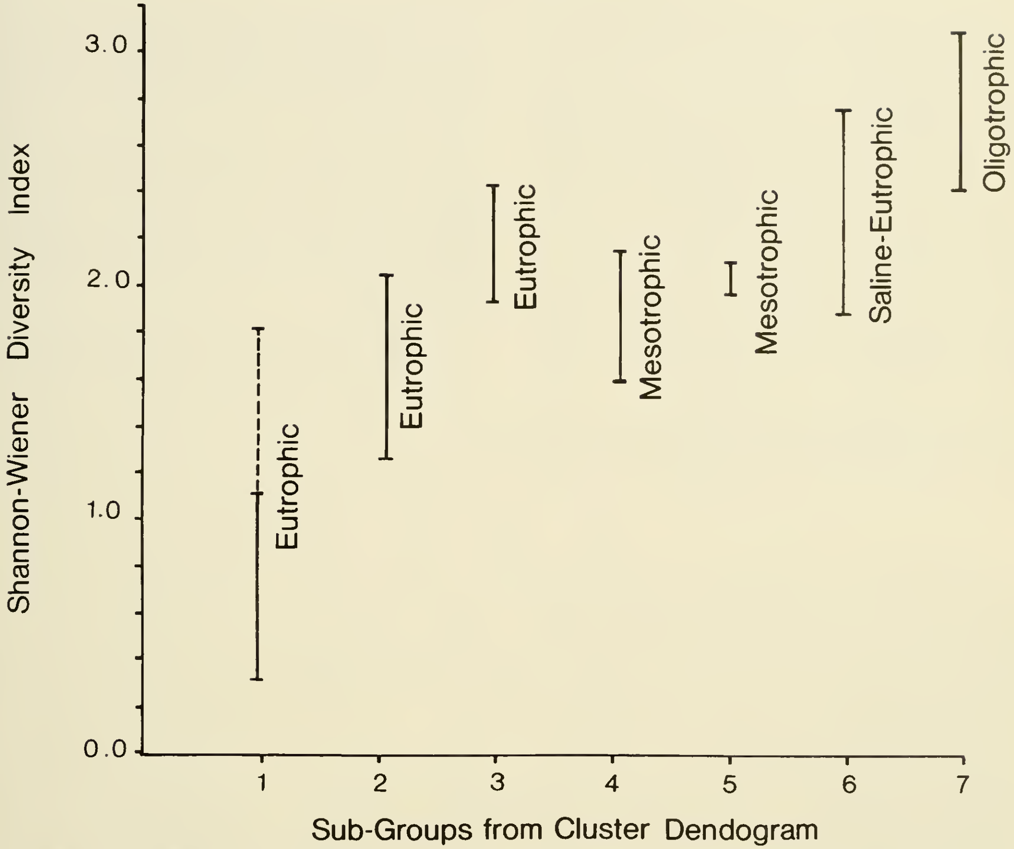

Fig. 4. Shannon-Wiener diversity indices for stands in relationship to subgroups described in the stand cluster dendrogram (Fig. 3). Subgroups I to III represent the eutrophic samples. Subgroups IV and V represent the mesotrophic sites, subgroup VI the saline eutrophic, and subgroup VII the oligotrophic.

lake. The other, from the west shore of the lake, was possibly influenced by one of the numerous underwater springs.

Subgroup V (Fig. 3) is not formed from stands from any particular lake. Except for one Deer Creek Reservoir sample, the stands are from mesotrophic systems. Diatoms that characterize this group are *Fragilaria crotonensis, Asterionella formosa, Stephanodiscus astraea* var. *minutula, Melosira granulata, Stephanodiscus niagarae,* and *Stephanodiscus astraea.* These organisms were present in less abundance than in the eutrophic groups, and diversity was higher (Fig. 4).

Subgroup VI (Fig. 3) is a discrete unit from Utah Lake. All the Utah Lake samples clustered together in this unit except for the two in subgroup IV. *Melosira granulata* var. *angustissima, Stephanodiscus astraea* var. *minutula,* and *Cyclotella meneghiniana* dominated this group. *Amphora ovalis, Stephanodiscus niagarae,* and *Achnanthes minutissima* were common in the majority of samples. This pattern of high diversity (Fig. 4) in an otherwise eutrophic system seems to be typical of saline eutrophic systems with high TDS and turbidity.

Subgroup VII (Fig. 3) is another unit of dissimilar samples. Each of these samples contained a diverse diatom flora (Fig. 4), and no single species or group of species dominated. Diatoms important in stands of this subgroup were *Achnanthes minutissima, Nitzschia palea, Asterionella formosa, Navicula cryptocephala* var. *veneta, Surirella ovalis, Achnanthes lanceolata, Gomphonema olivaceum,* and *Nitzschia amphibia.* Diversity was very high, as is common in oligotrophic systems (Fig. 4).

One sample from Rockport Reservoir did not cluster with any subgroup at all. The diatoms that characterized this sample were

Diatoma vulgare and *Cymbella affinis*. *Melosira varians* and *Gomphonema olivaceum* were also common. This stand did not cluster with subgroup II or III even though it also derives from moderately eutrophic waters.

This study supports the suggestion that diatom assemblages occurring in recent bottom sediments can accurately reflect current trophic conditions of the waters of deposition. Furthermore, the study of bottom sediment diatom assemblages can be extremely useful since sampling can be done during any season. Nevertheless, we view the study of recent bottom sediment diatoms as an important additional tool rather than a replacement of other biological, physical, and chemical analyses.

This conclusion is important for another reason. Paleodiatomological studies have long assumed that diatom assemblages in sediments have reflected the ecological status of depositional waters. The present study provides additional evidence that this assumption is valid.

To demonstrate the relationship between bottom sediment diatoms and planktonic

TABLE 4. Prevalent diatom species responsible for the formation of subgroups in Figure 2. The importance value is obtained by multiplying frequency by average relative density.

	Subgroup I	Subgroup II	Subgroup III	Subgroup IV	Subgroup V	Subgroup VI	Subgroup VII
Species							
Stephanodiscus astraea	82.3	51.0	44.6	9.6		3.3	2.3
Asterionella formosa	4.7	26.4	2.6	3.6	19.2		6.8
Stephanodiscus niagarae	1.5	6.1			7.9	5.5	
Melosira granulata	1.4	4.0		2.3	8.3		
Cocconeis placentua var. *lineata*	1.2		18.4				2.4
Hantzschia amphioxys	1.0						
Fragilaria crotonensis		2.3			32.5		
Achnanthes minutissima		1.7	2.6	4.5	1.2	4.1	10.4
Nitzschia palea			4.7		1.1		6.8
Navicula cryptocephala var. *veneta*			2.9	1.0			5.1
Epithemia sorex			2.7				
Fragilaria capucina var. *mesolepta*			2.6				
Navicula lanceolata			2.4				
Nitzschia amphibia			1.8				
Nitzschia frustulum			1.5				
Synedra socia			1.3				
Navicula pupula			1.2				
Synedra ulna			1.2				
Stephanodiscus astraea var. *minutula*				66.2	14.2	14.2	
Diatoma vulgare				1.0			2.8
Stephanodiscus astraea					7.6		
Cyclotella bodanica					1.6		
Melosira granulata var. *angustissima*						23.2	
Cyclotella meneghiniana						12.3	
Amphora ovalis						6.1	
Pleurosigma delicatulum						4.3	
Amphora ovalis var. *pediculus*						3.5	
Surirella ovalis						2.3	5.0
Navicula graciloides						1.5	
Diploneis smithii						1.1	
Nitzschia linearis						1.0	
Achnanthes lanceolata							4.8
Gomphonema olivaceum							3.2
Nitzschia amphibia							3.0
Amphora veneta							2.8
Cocconeis placentula var. *euglypta*							2.8
Cymbella ventricosa							2.5
Gomphonema parvulum							1.8

TABLE 5. Number of species encountered and Shannon-Wiener species diversity index for each sample studied. Sample codes refer to station numbers established by Mountainland Association of Governments (MAG 1977a) and Uinta Basin Association of Governments (Merritt et al. 1977a).

Sample number	Sample code	No. of species in sample	Species diversity index
Steinaker Reservoir			
1	SN-2	14	1.58
2	SN-1	31	3.07
Starvation Reservoir			
3	SR-3	10	1.72
4	SR-5	14	1.83
Moon Lake			
5	M-2	31	3.02
Strawberry Reservoir			
6	SB-1	15	0.74
7	SB-2	11	0.55
8	SB-3	6	0.37
9	SB-4	27	1.09
10	SB-5-1	22	0.54
11	SB-5-2	21	0.59
12	SB-5-3	5	0.74
13	SB-6-1	33	1.45
14	SB-6-2	16	0.83
15	SB-6-3	19	0.30
16	SB-6-4	39	1.93
17	SB-6-5	18	0.58
18	SB-6-6	4	0.93
19	SB-7	30	1.96
20	SB-9-1	22	1.03
21	SB-9-2	5	0.62
22	SB-9-3	15	0.96
23	SB-10	60	1.81
24	SB-11	39	2.41
Echo Reservoir			
25	E-3	38	2.65
26	E-2	21	1.63
27	E-6	16	2.39
28	E-1	27	2.13
29	E-7	32	2.90
30	E-5	22	1.95
Rockport Reservoir			
31	R-5	22	0.33
32	R-1	15	1.00
33	R-3	17	1.67
34	R-2	24	1.30
35	R-3.5	24	2.60
Deer Creek Reservoir			
36	A-2	18	1.23
37	A-3	24	1.64
38	C-1	14	1.92
39	C-2	38	1.51
40	C-3	46	2.03
41	C-4	21	1.94
42	DC-14	16	0.40
43	DC-13	17	0.70
44	DC-15	35	1.86
45	DC-7	26	1.43
Utah Lake			
46	UL-13.5	24	2.37
47	UL-13	27	2.72
48	UL-6	21	2.23
49	UL-26.5	21	1.89
50	PB-3	26	2.09
51	UL-3	18	1.99
52	UL-11	16	1.99
53	UL-12.5	23	1.95

Table 5 continued.

floras, we are currently correlating the relative densities of the two in our study sites with physical and chemical parameters. Further research is planned in three areas. First, we want to assess the effects of in-lake diatom transport. Second, we want to determine the usefulness of recent bottom sediment diatom studies for determining small differences in trophic status in a single lake. And third, we are interested in pursuing the reason for dominance of centric diatoms in our eutrophic study sites in contrast to other forms elsewhere (Stockner 1972).

LITERATURE CITED

BOLLAND, R. F. 1974. Paleoecological interpretation of diatom succession in recent sediments of Utah Lake. Unpublished dissertation. Univ. of Utah, Salt Lake City, Utah.

BORTLESON, G. C., AND G. F. LEE. 1975. Recent sedimentary history of Lake Monona, Wisconsin. Water, Air and Soil Pollution 4:89–98.

CAIRNS, J., JR., AND K. L. DICKSON. 1971. A simple method for the biological assessment of the effects of waste discharges on aquatic bottom-dwelling organisms. J. Water Poll. Control 43(5):755–772.

DUTHIE, H. C., AND M. R. SREENIVASA. 1972. The distribution of diatoms on the superficial sediments of Lake Ontario. Proc. 15th Conf. Great Lakes Res. Internat. Assoc. Great Lakes Res. 45–52.

ENVIRONMENTAL PROTECTION AGENCY. 1976. Preliminary report on the lakes and reservoirs in the Uintah Basin, Utah, EPA Region 8. Nat. Eut. Survey, C. Env. Res. Lab., Corvallis, Oregon.

KAESLER, R. L., AND J. CAIRNS. 1972. Cluster analysis of data from limnological surveys of the upper Potomac River. Am. Midl. Nat. 88(1):56–67.

Kaczmarska, I. 1976. Diatom analysis of Eemian profile in freshwater deposits at Imbramowice near Wroclaw. Acta Palaeobotanica 17(2):3–34.

Margalef, R. 1958. Information theory in ecology. Gen. Syst. 3:36–71.

Merritt, L. B., S. R. Rushforth, R. N. Winget, and S. R. Andersen. 1977a. Water quality assessment of several major lakes and reservoirs of Summit, Utah, and Wasatch counties of Utah. Mountainland Association of Governments Technical Working Paper 14. Eyring Research Institute, Provo, Utah. 310 pp.

Merritt, L. B., R. N. Winget, S. R. Rushforth, R. Baumann, and S. R. Andersen. 1977b. Lake water quality survey and biological assessment of stream quality in the Uinta Basin Association of Governments area. Interim Output Report 4. Eyring Research Institute, Provo, Utah. 203 pp.

Mountainland Association of Governments. 1977a. Sampling station index for water quality sampling sites in Summit, Utah, and Wasatch counties. MAG Technical Working Paper 8A. Eyring Research Institute, Provo, Utah. 75 pp.

———. 1977b. Biological data for water quality sampling sites in Summit, Utah, and Wasatch counties. MAG Technical Working paper 8C. Eyring Research Institute, Provo, Utah. 309 pp.

Ruzicka, M. 1958. Anwendung mathematisch-statisticher methoden in der geobotanik (Synthetische bearbeitung von aufnahmen) Biologia, Batisl. 13:647–661.

St. Clair, L. L., and S. R. Rushforth. 1977. The diatom flora of the Goshen warm springs, ponds and wet meadows, Goshen, Utah. Nova. Hedwiga 28:353–425.

Sneath, R. H. A., and R. R. Sokal. 1973. Numerical taxonomy: principles and practice of numerical classification. W. M. Freeman Co., San Francisco. 573 pp.

Stockner, J. G. 1971. Preliminary characterization of lakes in the Experimental Lakes Area, northwestern Ontario, using diatom occurrence in sediments. J. Fish. Res. Bd. Canada 28:265–275.

———. 1972. Paleolimnology as a means of assessing eutrophication. Verh. Internat. Verein. Limnol. 18:1018–1030.

Stockner, J. G., and W. W. Benson. 1967. The succession of diatom assemblages in the recent sediments of Lake Washington. Limnol. Oceonogr. 12:513–532.

Warner, J. H., and K. T. Harper. 1972. Understory characteristics related to site quality for Aspen in Utah. BYU Sci. Bull., Biol. Ser. 16(2):1–20.

Whiting, M. C., J. D. Brotherson, and S. R. Rushforth. 1978. Environmental interaction in summer algal communities of Utah Lake. Great Basin Nat. 38:31–41.

METHODS AND MATERIALS FOR CAPTURING AND MONITORING FLAMMULATED OWLS

Richard T. Reynolds[1] and Brian D. Linkhart[2]

ABSTRACT.— Techniques for locating, capturing, and monitoring activities and movements of Flammulated Owls were developed during four years of study. Adults responded to imitated territorial song throughout the nesting season. Nests were found by noting vocalizations and behaviors associated with courtship-feeding and food transfers between the sexes. After fledging, broods were difficult to follow, unless the young or adults were radio-tagged. Adults and young were captured with noose poles, hoop nets, and mist nets. Backpack harnesses and tail-mounted transmitters were used on adults and backpacks on fledglings. Transmitter life was 30–40 nights.

The Flammulated Owl (*Otus flammeolus* [Kaup]) is a little-known insectivorous species (Ross 1969) associated with montane forests of western North America (Bent 1938, Winter 1974). One of the smallest owls in this region, it is probably migratory in the northern part of its range (Balda et al. 1975).

The Flammulated Owl is often found in association with mature ponderosa pine (*Pinus ponderosa*) or Jeffrey pine (*P. jeffreyi*) forests mixed with fir (*Abies* spp.), Douglas fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), or incense cedar (*Libocedrus decurrens*) (Johnson and Russell 1962, Bull and Anderson 1978, Marcot and Hill 1980, Reynolds pers. obs.). However, the owl has been recorded in forests of second-growth pine (Winter 1974), pinyon pine (*P. monophylla*) (Huey 1932), and aspen (*Populus tremuloides*) (Webb 1982). Because few studies have involved intensive nest searches, the extent of breeding in any of these forest types or ages is unknown.

The association of this owl with mature pine, a forest type that is heavily managed throughout the western United States, its dependence on cavities for nests, and reports that this species was not found in cutover forests (Marshall 1957, Phillips et al. 1964, Franzreb and Ohmart 1978), suggests that this owl and its habitat affinities need further research. Because reliable techniques for locating, capturing, and monitoring Flammulated Owls were not available, research on this species has progressed slowly.

We studied a nesting population of Flammulated Owls in a 4 km^2 area of mature ponderosa pine forest in central Colorado from 1980 to 1983. As many as six nesting attempts and from 6 to 10 presumably nonbreeding territorial males were observed or monitored each year on the area. We report techniques found useful for locating nests, capturing birds, and monitoring their movements and patterns of habitat use.

LOCATING OWLS

Breeding adults were located from early May to mid-September by imitating their territorial song (see Marshall 1939, Winter 1971, Marcot and Hill 1980). On calm nights, singing owls can be heard to 1 km distance. We found that males responded more commonly, but females will occasionally sing prior to egg laying and after fledging. Nesting males respond less and sing on their own (without artificial stimulation) less than nonnesting males.

Prior to egg laying, both males and females were found in the vicinity of their nests by listening for the food solicitation (begging) calls of females (raspy "meow"s) and location calls of males ("boop-boop, boop-boop") when they entered the area with food. Fledged young were located by listening for their food begging (throaty hiss) and the location calls of adults. For the first five nights after fledging, broods remained within 100 m (but usually beyond 50 m) of their nests.

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Thereafter, some broods moved to 1 km from the nests through a series of sporadic movements, each followed by several sedentary nights. We used six-volt flashlights to aid in observations of the owls.

LOCATING NESTS

To identify nests, we first located and marked all trees containing cavity entrances greater than 4 cm diameter. When possible, we used a cavity-peeper (DeWeese et al. 1975) to confirm the suitability of cavities for owls. All Flammulated Owl nest cavities on our study area were flat bottomed and 18–40 cm deep, with minimum entrance diameters of 4–10 cm.

Each potential cavity was observed for 10–15 minutes at night to determine occupancy. The first three hours after dusk were the best because feedings were most frequent then (up to 7 feedings/15 minutes). When males approached with food they gave location calls, and females often responded by begging from within the cavity. About midway through nesting, both males and females fed the young in the cavity after calling quietly during approach. These calls were audible to 100 m under good conditions. The best procedure for checking suspected cavities was to take a position so as to highlight cavity entrances against the sky in order that approaching birds could be seen.

CAPTURE AND HANDLING

Four techniques were used to capture adults. During pair bonding and courtship feeding, when females are relatively sedentary, we used a 6.4 m telescoping noose pole with a 12.5 cm diameter loop of coated stainless steel line attached (Zwickel and Bendell 1967) to snare her or the male from trees. After egg laying and before fledging, both sexes were captured by placing a small mist net over the cavity entrance. The mist netting was formed to a bag (30 cm deep) and was woven to a wire hoop (40 cm dia) attached to the end of a telescoping pole. After the young fledged, adults were captured by tethering one or more young to the ground adjacent to a 3 × 6 m mist net. The mist net, shaped to form an L by wrapping it around a midpole, was placed so that the tethered young were inside and about 1.5 m from the corner. The high frequency of feeding in the early evening affords many opportunities to capture the adults. Owlets were captured by removing them from nests or by snaring them with noose poles after they fledged. In some cases we enlarged cavity entrances with rasps and files to gain access. Mist nets were used to capture adults from day roosts that were less than 4 m high. Nets were placed downslope from the roosts and the birds were flushed into them by approaching from the upslope side.

Handling of Flammulated Owls presents few problems. Immediately after capture the birds may struggle, but within a short time they become docile and may fall into a sleep that requires a minute or two from which to awake once released. When birds were held for extended periods (e.g., attaching transmitters), we inserted the owl into a sock with the toe end cut out but tied shut. This protected the bird and permitted us to lay it aside when necessary. When finished, the tied end was loosened and the bird slipped through.

MONITORING NESTING ACTIVITIES

Because Flammulated Owls are quite tame, observations at the nest seemed to disturb them little. To determine diets and frequency of food delivery, we used a soft background light (gasoline lanterns) placed approximately 10 m from the nest. This permitted the use of binoculars to observe adults as they approached the nest. Because food items are transported in the bill, tripod-mounted cameras adjacent to the hole and pointed into the approach route were used to photograph food. Photos provided an excellent means of identifying Lepidoptera larvae and other arthropods.

ACTIVITIES AND MOVEMENTS

Radio telemetry was useful in obtaining information on behavior, home range size, habitat use, intra- and interspecific interactions, and population densities.

Transmitter weights should not exceed 3–5% of a bird's body weight (MacDonald and Amlaner 1980). Mean weights of males and females in our study were 53 and 58 g, respectively. Our transmitters weighed 2.3 g, measured 20 × 9 × 9 mm, and had a life of 30–40 days. Short transmitter life required that the birds be recaptured frequently. Transmission distances ranged from 100 to 800 m, the latter being under line-of-sight conditions. Preliminary results indicate males may move up to 800 m from nests.

Backpacks and tail-mounts were used to attach transmitters. Tail-mounted transmitters (Kenward 1978) were used on adults nesting in small cavities. The tail-mount is attached to the dorsal rachis of the central tail feathers with commercial hot-melt glue (Bruggers et al. 1981). To avoid getting glue on the uropygial gland, we kept the transmitters away from the body and used a minimal amount of glue (0.3 g is sufficient). A package that is too heavy (3.0 + g) might result in feather breakage or premature shedding. Tail-mounts were not used on fledglings until tail feathers were fully developed.

The backpack harness (Smith and Gilbert 1981) was used for fledglings and adults. We used the double-loop style with dimensions of 12.5 cm (circumference) for the neck strap, 3.5 cm (length) for the breast strap, and 15 cm (circumference) for the body strap and the criss-cross style (overall length of 21.0 cm). Polyester elastic braid (3.1 mm wide) was used for strap material. The transmitter was attached to the harness with hot-melt glue before fitting the harness on the owl.

We used a portable receiver and a hand-held yagi antenna to follow individuals. Headphones facilitated direction-finding during pursuit and bad weather. Because males foraged over 17–27 ha and made frequent trips to their nests, it was helpful to have a co-worker at the nest to communicate with a two-way radio the owls' time of arrival and direction of departure. Although following the owls with hand-held antennae required considerable effort, this method (as opposed to triangulation) allowed direct observations that enabled us to determine foraging behavior and habitat use.

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Literature Cited

Balda, R. P., B. C. McKnight, and C. D. Johnson. 1975. Flammulated Owl migration in the southwestern United States. Wilson Bull. 87:520–533.

Bent, A. C. 1938. Life histories of North American birds of prey. Part 2. U.S. Nat. Mus. Bull. 170. 466 pp.

Bruggers, R., J. Ellis, J. Sedgwick, and J. Bourassa. 1981. A radio transmitter for monitoring the movements of small passerine birds. Proc. Third Internat. Conf. Wildl. Biotelem. 3:69–79.

Bull, E. L., and R. G. Anderson. 1978. Notes on Flammulated Owls in northeastern Oregon. Murrelet 59:26–27.

DeWeese, L. R., R. E. Pillmore, and M. L. Richmond. 1975. A device for inspecting nest cavities. Bird Banding 46:162–165.

Franzreb, K. E., and R. D. Ohmart. 1978. The effects of timber harvesting on breeding birds in a mixed coniferous forest. Condor 80:431–441.

Huey, L. M. 1932. Two noteworthy records for California. Auk 49:107.

Kenward, R. E. 1978. Radio transmitters tail-mounted on hawks. Ornis Scand. 9:220–223.

Johnson, N. K., and W. C. Russell. 1962. Distributional data on certain owls in the western Great Basin. Condor 64:513–514.

MacDonald, D. W., and C. J. Amlaner, Jr. 1980. A practical guide to radio tracking. Pages 143–159 *in* C. J. Amlaner, Jr., and D. W. MacDonald, eds., A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford.

Marcot, B. G., and R. Hill. 1980. Flammulated Owls in northwestern California. West. Birds 11:141–149.

Marshall, J. T., Jr. 1939. Territorial behavior of the Flammulated Screech Owl. Condor 41:71–78.

______. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pac. Coast Avifauna 32:1–125.

Phillips, A., J. T. Marshall, and G. Monson. 1964. The birds of Arizona. Univ. Ariz. Press, Tucson.

Ross, A. 1969. Ecological aspects of the food habits of insectivorous Screech Owls. Proc. West. Found. of Vert. Zool. 1:301–344.

Smith, D. G., and R. Gilbert. 1981. Backpack radio transmitter attachment success in Screech Owls (*Otus asio*). N. Amer. Bird Bander 6:142–143.

Webb, B. 1982. Distribution and nesting requirements of montane forest owls in Colorado. Part III: Flammulated Owl (*Otus flammeolus*). Colorado Field Ornithol. J. 16:76–81.

Winter, J. 1971. Some critical notes on finding and seeing the Flammulated Owl. Birding 3:205–209.

______. 1974. The distribution of the Flammulated Owl in California. West. Birds 5:25–44.

Zwickel, F., and J. F. Bendell. 1967. A snare for capturing Blue Grouse. J. Wildl. Manage. 31:202–204.

UTAH FLORA: CACTACEAE

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ABSTRACT.— The Cactaceae of Utah are revised. Keys to genera, species, and infraspecific taxa are provided. The taxa are provided with descriptions and geographical and other pertinent data. New nomenclatural combinations include *Sclerocactus pubispinus* (Englem.) L. Benson var. *spinosior* (Engelm.) Welsh and *Sclerocactus whipplei* (Englem.) Britt. & Rose var. *glaucus* (K. Schum.) Welsh.

Classification of cacti has been regarded as difficult, and our Utah taxa are not exceptions. Many factors combine to cause this difficulty. Morphologically similar flowers, at least in some of the genera, have forced workers to use vegetative characteristics such as stem and spine structure, nature of the areoles, presence or absence of surface coverings, shape and number of ribs or tubercles, and nature of hypogeous features for purposes of differentiation. Flowers, even within a taxon, may show great color amplitude. Additionally, workers have relied on the nature of the fruit, and, even in those years when fruits are formed, they are present for only a small portion of the year. The use of fruits by insects as incubation chambers for larvae makes this organ, in otherwise dry-fruited taxa, resemble fleshy fruits. Also, such infested fruits often are the only ones seen, as they persist after healthy fruits have matured and fallen.

Longtime workers in this field have typically used a common garden approach to avoid phenotypic variation as representing genotypic differences. But that approach has also led to problems because phenotypes in common garden grown plants sometimes lack similarity with the plants grown under field conditions, and attempts to identify field-grown plants by use of keys to identification based on the garden-grown ones often fail.

Paucity or lack of diagnostic reproductive morphology imposes a different kind of attempt at classification, wherein taxonomic groups are sometimes (perhaps often) based on analogies, not on homologies. Thus, the systems of classification of cacti tend to be artificial, with the taxonomic units sometimes representing convenience rather than relationship. The plants with vegetative parts appearing alike can have separate possible origins, and because they look alike they are placed together—though they might be but distantly related or completely unrelated. Possibly because of the artifical nature of the taxa, there are more infraspecific taxa than would seem warranted in other families of similar size; in Utah we have 28 species and 20 varieties, or a total of 48 taxa. Eleven of the species, or about 40 %, have two or more varieties.

Problems likewise involve breeding systems in the cacti. Hybridization is rampant in some genera, especially so in *Opuntia*, subgenus Opuntia, where almost every conceivable combination of hybridity is available in the field and is represented by specimens in the herbarium. Genetic barriers to hybridization seem to be lacking or essentially so. The plants, once established, have a great potential longevity. The presence of heterozygosity does not seem to affect that longevity, and it may increase the possibility of survival in more diverse habitats.

Problems of understanding cactus taxonomy have not been aided by the attraction of cacti to a large group of more or less well-trained admirers, some of whom have attempted, with varied success, to resolve nomenclatural and taxonomic difficulties. Some workers have studied the group from afar, and each variant has seemed worthy of being named. The named entities are then sought by other cactus fans, in an extension of the trophy syndrome. Professional workers in the family have sometimes attempted to diminish collecting by trophy hunters and commercial gatherers by withholding information on collection localities, making further legitimate work difficult if not impossible. Into this tangled jungle of nomenclatural and taxonomic problems struggled Lyman Benson, whose life work on the cacti (1982) represents the first overview of the family for North America north of Mexico and the most realistic approach to undoing the Gordian knot created by all those who had worked with the group prior to him. Because of his tremendous contribution to an understanding of the Cactaceae, this meager work is dedicated to him.

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Tolerance to varied ecological conditions evidently results in different phenotypical responses, even when the genotype is more or less homogenous. Thus, plants from shaded slopes may have a different appearance than those in the more open area nearby.

Ecologically many of the cactus species are opportunists, taking advantage of reduction of more palatable range vegetation, thereby increasing under heavy utilization by livestock in some areas. Cacti are thought of as indicators of drought situations, but some species show great ecological amplitude, occurring from dry low elevation areas upward to mesic high elevation sites. The greater bulk of them occur in the southernmost counties, especially in Washington County with its extension of the Mojave Desert vegetative type. Cacti are present in every county in Utah, however.

Cacti are generally armed with spines, which are straight, curved, or twisted; erect, spreading, or deflexed; smooth or barbed; variously colored; flattened or terete; or in some species and forms lacking altogether. The spines serve to protect the plants from predation and grazing by inflicting mechanical injury to animals and humans. Some birds, however, have learned to take advantage of certain of the cacti by building nests among the protective curtain of spines, i.e., the cactus wren. The opuntias have other features that protect them. In subgenus Cylindropuntia the epidermis of the spines is deciduous, forming a sheath that remains within the puncture wound when animals contact the sharp spines. Additionally, all opuntias produce neatly packed multirowed, retrorsely barbed spinules known as glochids. The glochids are borne in the upper portion of the areoles, specialized areas at the nodes (often on tubercles). This upper portion of the areole is also the area capable of continued growth, and new glochids seem to form each year on some *Opuntia*. The glochids are easily detachable by even gentle contact with animal skin. The sharp points penetrate the skin and are locked in place by the retrorse barbs, forming a subvisible burning irritant that reminds one of its presence with each contact with some surface, even following diminution of the initial burning sensation.

Because of their form, armament, and ability to hold water, usually as bound water in complex colloidal systems, botanists have been reluctant to make collections. The present study is based on the examination of 606 specimens, and the writer has collected only 173 of those. The preservation of an adequate herbarium specimen requires time, patience, and suffering. Because of these problems, and because the specimens thus produced are often offensive to the aesthetic senses of botanists, they are collected only by persons of great devotion or dullness. Hence, botanical collection seldom provides much voucher material for definitive taxonomic judgments, and little possibility exists of depletion of natural populations by botanical collectors. The cacti are a miserable group with which to work and, except as botanical curiosities, they would have received little attention.

Fortunately, commercial gathering of cactus species in Utah has not been extensive. Our marketable cacti are few, and with one or two exceptions there seems to be little future in gathering cacti commercially in Utah.

The flowers of cacti are, however, among the most beautiful of all plants in Utah. The numerous petals (petaloids) vary from white to yellowish, greenish, yellow, golden, bronze, pink, violet, pink-purple, violet-purple, red, and scarlet, each taking on an almost fluorescent hue due to shape of individual cells in their surfaces. Photographs seldom do justice to the beauty of the plants; they are best viewed in their natural habitats, where the mind serves to judge the intense beauty and to hold that vivid impression in memory.

CACTACEAE

Cactus Family

Perennial succulent woody or herbaceous plants, with spiny, glochidiate, or rarely unarmed, globose, cylindric, columnar, or flattened stems; stems ribbed, smooth, or tuberculate; leaves lacking, or green, terete, and caducous (*Opuntia*); areoles axillary (regardless of apparent position), bearing wool, glochids, spines, branches, or flowers; perianth of numerous segments grading from sepals to petals, imbricate, the bases more or less united, inserted on a hypanthium; stamens numerous, variously inserted within the hypanthium tube; style 1; stigmatic lobes several; ovary inferior; fruit a dry or fleshy many-seeded berry.

Benson, L. 1982. The cacti of the United States and Canada. Stanford Univ. Press, California. 1044 pp.

1. Stems jointed, the joints flattened, clavate, or cylindric; areoles with glochids and spines (or spineless), subtended by caducous terete green leaves when young .... *Opuntia*

— Stems hemispheric or cylindroid, not jointed; areoles with hair or spines but no glochids 2

2(1). Flowers borne in axils of tubercles or at bases of grooves, removed from the spiniferous areoles; central spine hooked, dark purple; small hemispheric or cylindrical plants of Washington County .... *Mammillaria*

— Flowers borne variously, seldom as above; central spines hooked or straight, but if hooked then not of Washington County 3

3(2). Stems with tubercles spirally arranged; tubercles distinctly grooved on upper side; flowers pink or yellow .... *Coryphantha*

— Stems ribbed; tubercles not grooved; flowers variously colored 4

4(3). Flowers borne laterally below the stem apex; hypanthium spiny .... *Echinocereus*

— Flowers terminal on the stems; hypanthium devoid of spines 5

5(4). Stems 20–50 cm in diameter or more, mainly 2–10 dm tall; upper axils and ovaries not woolly; plants of Washington County .... *Ferocactus*

— Stems usually much smaller, or if, as rarely, approaching the lower limits as described above, the ovaries and upper axils woolly 6

6(5). Stems mainly 12–25 cm in diameter; spines flattened, annular; ovaries and upper axils woolly; plants rare in Kane (?) and Washington counties .... *Echinocactus*

— Stems mainly 3–10 cm in diameter; spines variously terete, subterete, or flattened, but not annular; ovaries and upper axils not or rarely woolly 7

7(6). Spines straight, purplish or reddish, 2–5 cm long or more; flowers rose-pink; plants of the Beaver Dam Mountains, Washington County .... *Neolloydia*

— Spines hooked or some or all of them straight; flowers variously colored; plants not of western Washington County, or if so then the flowers yellow 8

8(7). Stems with spines all straight, depressed-hemispheric; flowers white to yellow or pale pinkish, mainly 1–2 cm long .... *Pediocactus*

— Stems with at least some spines hooked, or if straight, then flowers rose-pink to violet or more than 2 cm long .... *Sclerocactus*

CORYPHANTHA (Engelm.) Lem.

Plants depressed-hemispheric to hemispheric or shortly cylindric, solitary or colonial; tubercles separate; areoles circular; spines smooth; central spines 0 or 3–12 per areole, transitional to radials, straight, elliptic in cross-section; radial spines 12–40 per areole, straight, subterete; flowers axillary at tubercle base, at end of a felty persistent groove connected to the areole, borne near the summit of the stem; flowers funnelform, the perianth pink-purple to rose or yellow; fruit fleshy, green or red, indehiscent; seeds black or brown.

1. Flowers yellow; fruit red at maturity, globular; plants rare in Garfield and Kane counties .... *C. missouriensis*
— Flowers pink-purple to rose; fruit green at maturity, ellipsoid; plants widely distributed .... *C. vivipara*

Coryphantha missouriensis **(Sweet) Britt. & Rose** [*Mammillaria missouriensis* Sweet]. Stems commonly solitary, depressed hemispheric, 2–5 cm tall, 3–8 cm wide; tubercles 6–9 mm long; areoles few; radial spines 10–19, spreading; flowers 3.8–5 cm wide and long; sepaloids greenish, the margins yellowish or whitish; petaloids yellow; filaments yellow; anthers yellow; style green, 12–25 mm long; fruit red, ca 1 cm thick; seeds black, 2–2.5 mm wide. Cool desert shrub, juniper, and ponderosa pine communities in Garfield (type of variety from Hells Backbone) and Kane (lectotype of variety from Buckskin Mts.) counties; Arizona. Our material belongs to **var. *marstonii*** **(Clover) Benson** [*C. marstonii* Clover]; 1 (0). The species is distributed from Montana east to North Dakota, south to Arizona, New Mexico, and Texas.

Coryphantha vivipara **(Nutt.) Britt. & Rose** [*Cactus viviparus* Nutt.]. Stems solitary or colonial, depressed hemispheric to short-cylindric, mainly 2–15 cm tall, 2–10 cm wide; tubercles 6–9 mm long; areoles 1.5–3 mm wide; central spines 3–12, whitish basally, dark apically, mainly 12–20 mm long; radial spines 12–20, spreading, obscuring the stem; flowers 2.5–5 cm wide and long; sepaloids greenish, the margins variously colored; petaloids pink-purple or rose; anthers yellow; fruit green, ellipsoid, 12–25 mm long; seeds brown, reticulate, 1.5–2 mm wide. Three more or less distinctive varieties are present in Utah.

1. Central spines 4; flowers ca 3.8 cm wide; plants of Carbon and Uintah counties .... *C. vivipara* var. *vivipara*
— Central spines 4–7; flowers wider or if narrower then not of northeastern Utah 2
2(1). Flowers about 2.5–3 cm wide; radial spines 12–20, 9–12 mm long; petaloids yellowish, greenish, or pinkish; plants of Washington County ..*C. vivipara* var. *deserti*
— Flowers mainly 3.8–5 cm wide; radial spines 20–30; petaloids pink-purple to rose; plants rather broadly distributed .... *C. vivipara* var. *arizonica*

Var. *arizonica* **(Engelm.) W. T. Marshall** [*Mammillaria arizonica* Engelm.]. Desert shrub and pinyon-juniper communities at 1586 to 2440 m in Beaver, Garfield, Juab, Kane, Millard, Piute, San Juan, Sevier, Tooele, Washington, and Wayne counties; Nevada to Colorado, south to Arizona and New Mexico; 23 (xiii). This variety is locally common on limestone and dolomite outcrops and on gravels degraded from them. It is a beautiful plant when in flower, the violet flowers contrasting with the thatch of whitish spines. Like other of our depressed-hemispheric cacti, the plants expand as they take up water in springtime. Following flowering, the plants dry and shrink downward into the substrate surface. Plants conspicuous at flowering become difficult to observe when dormant. The juice of *Coryphantha vivipara* is apparently unique among our species in being non-mucilaginous.

Var. *deserti* **(Engelm.) W. T. Marshall** [*Mammillaria deserti* Engelm; *M. chlorantha* Engelm., type from St. George]. The small yellowish to pinkish flowers are apparently diagnostic. Warm desert shrub communities at 760 to 980 m in Washington County; Arizona, Nevada, and California; 2 (i).

Var. *vivipara*. Desert shrub and pinyon juniper communities in Carbon and Duchesne counties; Alberta to Manitoba, south to Oregon, New Mexico, and Texas; 1 (0).

ECHINOCACTUS Link & Otto

Stems solitary or few to many, subglobose to cylindric, woolly at the apex, few- to many-ribbed; areoles large; spines broad, flattened-triangular, with transverse annular rings; flowers borne subapically, yellow; floral tube bearing spiny persistent scales; ovary clothed with narrow scales having mats of wool; fruit densely white-woolly, dry at maturity; seeds black, shining.

***Echinocactus polycephalus* Engelm. & Bigel.** Stems mostly 2–3 dm tall and 1–2 dm thick (or more); ribs 10–21; areoles 10–12 mm long; radial spines 8–10, 2.5–5 cm long, often reddish when young, subulate, triangular-flattened; central spines 3–5, stouter than the radial, annulate, curved but not hooked, 3–8 cm long; flowers 5–6 mm long, yellow; perianth segments narrowly oblong; fruits 15–25 mm long, dehiscing by a basal pore; seeds angular, black. Two varieties are potentially present in Utah.

1. Spines felty, at least when young; seeds papillate, dull or shining from the papillae; plants of Washington County .... *E. polycephalus* var. *polycephalus*
— Spines smooth or with scattered hairs; seeds smooth and shining; plants of Kane (?) County .... *E. polycephalus* var. *xeranthemoides*

Var. *polycephalus*. Warm desert shrubland on the Beaver Dam slope, Washington County (reported by Meyer); Nevada, California, and Arizona; 0 (0).

Var. *xeranthemoides* Coulter. Pinyon-juniper and desert shrub communities near Kanab, Kane County, Arizona; a Plateau endemic; 0 (0). This report is based on two collections by pioneer collectors, one by A. L. Siler (in "Kanab Mts.") in 1881 and the other by Dr. E. Palmer in 1877 (in "S. Utah"). Since it is probable that neither knew where the Utah-Arizona boundary was situated (it was surveyed in 1879), the collections noted could have been taken from nearby Arizona. However, the plants should be sought near Kanab.

ECHINOCEREUS Engelm. in Wisliz.

Stems erect or ascending, solitary or more usually colonial, cylindric or subcylindric; areole small; central spines 1–6; radial spines 5–12, acicular to subulate, flattened or subterete; flowers borne laterally, below the stem apex, the bud breaking through the epidermis above the areole, large and showy, pink-purple to scarlet; stigmas green; fruit fleshy, spiny, not regularly dehiscent, the spine clusters deciduous as fruit matures.

1. Flowers pink-purple to rose; stems solitary or few, often over 10 cm tall .... *E. engelmannii*
— Flowers scarlet; stems often 10 cm long or less, few to numerous in compact hemispheric clusters .... *E. triglochidiatus*

***Echinocereus engelmannii* (Parry) Lem.** [*Cereus engelmannii* Parry]. Stems solitary or 2 to several (or rarely many) and loosely clustered, mainly 10–30 cm tall, 5–9 cm thick; ribs 10–13; tubercles not prominent; areoles small, subcircular; central spines 2–6, stout, more or less curved or twisted, 2–5 cm long; radial spines 6–12, 7–15 mm long, appressed and spreading; flowers 5–9 cm long, pink-purple to rose; perianth segments oblong; fruit ovoid to oblong, green or turning red, the spine clusters deciduous; seeds black, globose, pitted, 1–1.5 mm long. This widely ranging southwestern species consists of a series of morphologically differing but intergrading segregates, which largely lack geographical integrity. Utah material has been assigned to three of the named segregates (Benson 1982). The following tentative key will serve to allow application of names to most specimens.

1. General aspect of spines purplish-black, with some grayish ones apically or intermixed; stems mainly 15–30 cm tall; plants of warm desert shrub communities in south central Washington County ...... *E. engelmannii* var. *purpureus*

— General aspect of spines grayish, with some purplish black ones apically or intermixed; stems often 10–20 cm tall; plants of various distribution 2

2(1). Lowermost central spines mainly 3.5–6 cm long, not markedly differing in color from the other spines; plants of canyons of the Colorado .... *E. engelmannii* var. *variegatus*

— Lowermost central spines mainly 2.8–4.5 cm long, often markedly differing in color from other spines; plants mainly not of the Colorado canyons .... *E. engelmannii* var. *chrysocentrus*

Var. *chrysocentrus* (Engelm. & Bigel.) Engelm. ex Rumpler [*Cereus engelmannii* var. *chrysocentrus* Engelm. & Bigel.]. Larrea, Joshua tree, shadscale, and mountain brush communities at 760 to 1865 m in Beaver, Juab, Kane (inter var. *variegatus*), Millard, and Washington counties; Nevada, California, and Arizona; 18 (v).

Var. *purpureus* L. Benson Blackbrush community at 915 to 1130 m in south central Washington Co. (type from 1 mi N St. George); endemic; 16 (i). This dark-spined phase of hedgehog cactus is transitional to var. *chrysocentrus*. Interpreted broadly, it includes specimens from near Leeds to west of Santa Clara, and might be regarded as a dark-spined phase of var. *chrysocentrus*. But the degree of integrity is about the same as for infraspecific taxa elsewhere in the Cactaceae, and it seems best to recognize this entity at some taxonomic rank.

Var. *variegatus* (Engelm. & Bigel.) Engelm. ex Rumpler [*Cereus engelmannii* var. *variegatus* Engelm. & Bigel.]. Blackbrush, shadscale, and pinyon-juniper communities at 1125 to 1895 m in Garfield, Kane, and San Juan counties; Arizona; 6 (ii). Purported differences between this phase of the species complex and those noted for var. *chrysocentrus* are tenuous, and the two phases could be combined without doing serious injustice to their taxonomy.

***Echinocereus triglochidiatus* Engelm.** [*E. coccineus* Engelm.]. Stems few to several hundred in compact hemispheric clumps or mounds, mainly 8–15 cm long, 3–6 cm thick; ribs 9 or 10, the tubercles not prominent; areoles circular, bearing a white felty mat when young; central spines 1–3, 8–40 mm long or more, stout, straight or curved to twisted; radial spines 5–8, 4–35 mm long, not appressed, spreading; flowers 5–7.5 mm long, scarlet; perianth segments cuneate-obovate; fruit red at maturity, obovoid to cylindroid; seeds papillate, 1.5–2 mm long. Three rather weakly separable varieties are present in Utah.

1. Areoles spineless or with spines less than 3 mm long; plants of San Juan and adjacent Grand counties .... *E. triglochidiatus* var. *inermis*

— Areoles armed, the spines mainly 4–40 mm long or more; plants of broad but different distribution 2

2(1). Central spines twisting or curved; flowers often over 4 cm wide; plants of Millard, Beaver, and Washington counties .... *E. triglochidiatus* var. *mojavensis*

— Central spines straight; flowers often less than 4 cm wide; plants of broad distribution .... *E. triglochidiatus* var. *melanacanthus*

Var. *inermis* (K. Schum.) Rowley [*E. phoeniceus* var. *inermis* K. Schum.]. Salt desert shrub-pinyon-juniper vegetative types at ca 1525 m in San Juan and Grand (?) counties; Colorado; a Plateau endemic; 1 (i). The type was taken from the La Sal Mts. Benson (1982) treats this plant in synonymy under var. *melanacanthus*, but it has about the same degree of morphological and geographic integrity as do other phases regarded as varieties. It is recognized herein mainly to draw attention to its existence.

Var. *melanacanthus* (Engelm.) L. Benson [*Cereus coccineus* var. *melanacanthus* Engelm.]. Blackbrush, Ephedra, sagebrush, pinyon-juniper, mountain brush, and aspen communities at 975 to 2562 m in Beaver, Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, Piute, San Juan, Sanpete, Sevier, Tooele, Uintah, Utah, Washington, and Wayne counties; Nevada to Colorado, south to California, Arizona, New Mexico, Texas, and Mexico; 77 (xiii).

Var. *mojavensis* **(Engelm. & Bigel.) L. Benson** [*Cereus mojavensis* Engelm. & Bigel.]. Mixed desert shrub, pinyon-juniper, and ponderosa pine communities at 1550 to 2257 m in Beaver, Millard, and Washington counties; 3 (i).

FEROCACTUS Britt. & Rose

Plants hemispheric to cylindric, massive; ribs thick, prominent, somewhat spirally arranged; spines coarse, the central ones flattened and transversely annulate, not hooked; areoles large, more or less woolly when young; flowers subterminal, yellow, funnelform; stamens numerous; ovary and floral tube scaly, not woolly; fruit oblong in outline, dry at maturity, dehiscent by a basal pore.

Ferocactus acanthodes **(Lem.) Britt. & Rose** [*Echinocactus acanthodes* Lem.]. Plants mainly 2–15 dm tall and 2–5 dm thick or more; ribs 20–30; areole 1–1.5 cm long, brown-woolly when young; spines pink, red, or yellow, the central ones 1–4, subulate, flattened, annulate, curved, 4–8 cm long or more; radial spines with mixed coarse and slender ones; flowers 4–6 mm long, the scales of the tube and ovary overlapping when young, ovate; perianth segments oblong to spatulate; filaments yellow; fruit 3–3.5 cm long; seeds 2–3 mm long, reticulate. Limestone and dolomite outcrops and gravels at 760 to 1375 m in Washington County; Nevada, California, and Arizona; 1 (0). Our material belongs to var. ***lecontei*** **(Engelm.) Lindsay** [*Echinocactus lecontei* Engelm.]. This is the largest cactus native to Utah; it is distinguished from *Echinocactus polycephalus* by the large size, glabrous ovaries, and merely short-woolly areoles.

MAMMILLARIA Haw.

Subglobose to shortly cylindric plants, stems solitary or few; tubercles many, elongate, in spiral rows; areoles spiniferous; spines smooth, the central 1–4 straight or 1 or more hooked; flowers borne between tubercles, diurnal; fruit fleshy, red, lacking appendages, elongate.

Mammillaria tetrancistra **Engelm.** [*Phellosperma tetrancistra* (Engelm.) Britt. & Rose.]. Stems 4–10 cm tall or more, 4–6 cm wide; tubercles 4–10 mm long, more or less woolly in the axils when young; central spines 1–4, dark, 1 or more hooked, 10–15 mm long; radial spines 30–45, mostly whitish; flowers 25–30 mm long; sepaloids green with pink margins; petaloids rose to pink-purple; fruit scarlet, 12–20 mm long. Warm desert shrub communities at 760 to 1300 m in Washington County; Nevada, California, Arizona; 3 (ii).

NEOLLOYDIA Britt. & Rose

Subglobose to shortly cylindric plants, mostly solitary; ribbed and more or less tuberculate; areoles small; central spines 1 to several or lacking, straight (or curved), not hooked; radial spines 9–10; flowers borne subapically at the base of a woolly groove, purple or pink-purple; fruit green, drying tan, dehiscing by a basal pore, the scales and their axils glabrous.

Neolloydia johnsonii **(Parryi) L. Benson** [*Echinocactus johnsonii* Parry in Engelm.; *Echinomastus johnsonii* (Parry) Baxter; *Ferocactus johnsonii* (Parry) Britt. & Rose]. Stems solitary, seldom branched, 8–20 cm tall, 5–10 cm thick, the ribs 17–21, obscured by interlocking spines; areoles with a short narrow woolly groove running to the axil; central spines pink to reddish or purplish, 3–4 cm long, terete; radial spines paler in color; flowers 5–6 cm long, purple or pink-purple; fruit green, drying tan, oblong, 10–15 mm long, nearly naked, splitting dorsally; seeds ca 2.5 mm long, papillate. Warm desert shrub community at 760 to 1250 m in Washington County; Nevada, Arizona, and California; 3 (i).

OPUNTIA Mill.

Stems jointed, the joints flattened, cylindric, or clavate; areoles with glochids (i.e., detachable barbed spinules), and commonly with 1 or more stout spines (less commonly spineless); spines naked or sheathed; leaves terete, fleshy, caducous; flowers borne in areoles of previous year's growth, variously colored; floral tube cup shaped; ovary with areoles; stamens numerous; stigmas short; fruit fleshy or dry, armed or unarmed; seeds with a bony aril, flattened.

1. Stem joints cylindric or clavate; spines with detachable epidermal sheaths, at least apically (subgenus Cylindropuntia) 2

— Stem joints flattened; spines not sheathed (subgenus Opuntia) 5

2(1). Stem joints clavate, 1 or few above ground, mainly 3–10 cm tall, arising from a tuberous subterranean joint; plants of Millard, Juab, and Tooele counties .... *O. pulchella*

— Stem joints cylindric, several to numerous above ground, mainly 3–20 dm tall, not arising from a tuberous joint; plants of various distribution 3

3(2). Joints mainly less than 2 cm thick; fruits fleshy at maturity; plants of rather broad distribution in Utah .... *O. whipplei*

— Joints mainly over 2.5 cm thick; fruits dry at maturity; plants mainly of Washington County 4

4(3). Ridge of tubercle on mature joints mainly 18–22 mm long, more than 3 times longer than broad; longer terminal joints mainly more than 15 cm long .... *O. acanthocarpa*

— Ridge of tubercle on mature joints mainly 10–15 mm long, only 1–2 times longer than broad; longer terminal joints mainly shorter than 15 cm long .... *O. echinocarpa*

5(4). Areoles with glochids only; spines not developed (except in hybrids with other taxa), or if present the glochids very numerous and 4–10 mm long; plants of Washington, Kane, and San Juan, and less commonly of Emery, Garfield and Wayne counties .... *O. basilaris*

— Areoles with glochids and spines, at least some, or if lacking (a condition probable in all species) then of different distribution 6

6(5). Fruit dry at maturity, finally tan, green or reddish when young; seeds mainly 4–8 mm long, rough and irregular in outline (key nonfruiting specimens both ways) 7

— Fruit fleshy at maturity, red or reddish purple to purple; seeds mainly 2.5–4.5 mm long, smooth and regular in outline 10

7(6). Largest joints 2–8 cm long, 1.5–3.5 cm wide, readily detachable (carried burrlike by animals) .... *O.fragilis*

— Largest joints mainly 7–15 cm long or more, 4–12 cm broad or more, not readily detachable 8

8(7). Spines not especially flattened, even basally, terete or nearly so, or rarely lacking; plants transitional to the next .... *O. polyacantha*

— Spines at least somewhat flattened, at least basally, usually elliptic in cross-section 9

9(8). Spines less than 1 mm thick, more or less flexible; joints mainly 5–15 cm long and 3–10 cm wide; plants rather widespread, transitional to the next .... *O. erinacea*

— Spines over 1 mm thick (at least some), not especially flexible; joints often over 15 cm long and 10 cm wide; plants of the Glen Canyon vicinity (transitional to *O. phaeacantha*) .... *O. nicholii*

10(9). Spines terete to subterete, not flattened (except when hybridizing with *O. phaeacantha*), commonly 1–6 per areole 11

— Spines at least basally flattened, narrowly elliptic in cross-section, commonly 3 per areole 12

11(10). Spines gray or brownish; plants usually prostrate, not forming upright clumps; largest joints mainly less than 12 cm long; plants scattered in Utah ...... *O. macrorhiza*

— Spines tan or variously colored; plants usually upright and with several joints standing above the ground; largest joints mainly more than 12 cm long; plants of San Juan and Washington counties .... *O. littoralis*

12(10). Joints subcircular in outline; spines all deflexed, yellow; plants of Washington County .... *O. chlorotica*

— Joints mainly obovate in outline; spines spreading in various directions, brown to tan or gray; plants of rather broad distribution .... *O. phaeacantha*

Opuntia acanthocarpa **Engelm. & Bigel.** Shrubs, mainly 8–15 dm tall or more; trunk short; larger terminal joints mostly 12–50 cm long, 2–3 cm thick; tubercles decurrent along the joint, mostly 15–50 mm long and 4–6 mm wide; leaves caducous; areoles circular; spines 6–20 or more per areole, 1–4 cm long, variously colored, the sheathes straw colored; glochids minute; flowers 4–6 cm long; sepaloids greenish yellow; petaloids red, purplish, or yellow; ovary spiny; fruit dry, tan or brown, spiny, 2–4 cm long; seeds 5–8 mm long, tan or whitish. Larrea-Joshua tree, and other warm desert shrub communities at 760 to 1220 m in Washington County; Nevada, California, Arizona, and Mexico; 5 (i). Two varieties are reported from Utah by Benson (1982); **var. *acanthocarpa*,** with tubercular ridges 30–50 mm long and longer joints 25–50 cm long; and **var. *coloradoensis* L.** Benson, with tubercular ridges 15–22 mm long and larger joints 12–30 cm long. More material is necessary to determine the nature of the Utah materials.

Opuntia basilaris **Engelm. & Bigel.** Plants mainly 10–30 cm high and to 1 m broad or more; joints blue, blue-green, violet-green, or green, obpyriform, obovate, orbicular, or spatulate, 5–30 cm long, 2.5–12 cm broad; areoles circular, 9–17 mm apart; spines lacking (some present in various hybrids); glochids brown to tan; flowers 5–8 cm long; sepaloids greenish, edged with violet or yellow; petaloids violet or yellow; fruit 2.5–3 cm long, dry at maturity, green, becoming tan or gray; seeds ca 6–8 mm long, white or grayish. Four more or less distinctive and geographically correlated, but problematical, varieties are present.

1. Joints obpyriform, seldom otherwise, suffused with violet or blue; glochids brown; plants of Washington and San Juan counties .... *O. basilaris* var. *basilaris*

— Joints mainly obovate to spatulate, suffused with blue, or green or yellow; glochids tan to yellowish; plants variously distributed 2

2(1). Spines often present; glochids mainly 4–10 mm long, often copious; plants of Washington County, transitional to *O. phaeacantha* .... O. basilaris var. *woodburyi*

— Spines lacking or essentially so; glochids seldom to 4 mm long, moderately abundant; plants of various distribution 3

3(2). Joints obovate, bluish green (drying ashy or bluish); flowers commonly yellow; plants of Kane and Washington counties .... *O. basilaris* var. *aurea*

— Joints spatulate, yellowish to bluish green; flowers commonly violet; plants of Emery, Garfield, and Wayne counties .... *O. basilaris* var. *heilii*

Var. *aurea* **(Baxter) W. T. Marshall** [*O. aurea* Baxter, type from Pipe Springs, Arizona]. Sagebrush, pinyon-juniper, and ponderosa pine communities at ca 1220 to 2075 m in Kane and Washington counties; Arizona; a Plateau endemic; 6 (iii). Intermediates occur between this taxon and *O. erinacea* and *O. polyacantha*.

Var. *basilaris*. Warm desert shrub community at 760 to 1770 m in San Juan (Cataract Canyon) and Washington counties; Nevada, California, Arizona, and Mexico; 10 (iv). The materials from Cataract Canyon differ in tenuous ways from the typical material in Washington County; they do not seem worthy of taxonomic recognition.

Var. *heilii* Welsh & Neese. Salt desert shrub communities at 1460 to 1680 m in Emery, Garfield, and Wayne counties; endemic; 3 (0).

Var. *woodburyi* Earl. Warm desert shrub community at ca 920 m in Washington County (type from Fort Pierce Wash); endemic; 4 (i). This "variety" appears to have been derived from introgression involving *O. basilaris* var. *basilaris* and *O. phaeacantha*, which are sympatric at the type locality (N. D. Atwood, pers. comm.). The plants are long lived and form a portion of the diversity within the opuntias of Washington County. Recognition at taxonomic rank is problematical for two reasons; naming of hybrid derivatives could proceed endlessly, and the dilemma of placement of the "variety" in one of the parental species begs the question of the contribution of the other parent (i.e., it is allied to both, but it cannot be placed in both).

***Opuntia chlorotica* Engelm. & Bigel.** Shrubby plants, mainly 6–15 dm tall; trunk to 30 cm long; larger joints 15–20 cm long and about as broad, orbicular to suborbicular, blue-green; areoles elliptic, ca 20 mm apart; spines present in all but basal areoles, yellowish, 1–6, all deflexed, straight or curved at the base, 2.5–4 cm long; glochids yellow; flowers 5–8 mm long; sepaloids and petaloids yellow, or suffused with red; ovary with glochids and some spinules; fruit fleshy, grayish, tinged with purple, lacking spines; seeds 2.2–3 mm long, tan, smooth. Desert shrub communities at 1400 m in Washington County (Beaverdam Mts. and Zion Canyon); Nevada, California, Arizona, New Mexico, and Mexico; 3 (ii).

***Opuntia echinocarpa* Engelm. & Bigel.** Shrubs, mainly 8–15 dm tall; trunk to half of plant height; larger terminal joints mainly less than 15 cm long (5–15), 2–4 cm thick; tubercles decurrent along the joint, mostly 6–15 mm long and 4–5 mm wide; leaves caducous; areoles circular; spines 3–12 per areole, 1–3 cm long, straw colored or silvery or yellow; sheathes colored like the spines; glochids minute; flowers 3–4.5 cm long; sepaloids and petaloids greenish yellow, the outer sometimes suffused reddish; fruit dry, green, turning tan. Creosote bush, Joshua tree, blackbrush, and shadscale communities at 760 to 1376 m in Beaver (?) and Washington counties; Nevada, California, Arizona, and Mexico; 5 (iii).

***Opuntia erinacea* Engelm.** Plants mainly 10–30 cm tall and to 1 m in diameter or more; larger joints obovate to spatulate, glaucous, 5–19 cm long, 3–11 cm wide; areoles small, 4–18 mm apart; spines at all or most areoles or only in the upper ones (or lacking?), 4–9 per areole, deflexed, flexible, straight or irregularly curved, 0.5–10 cm long, less than 1 mm thick, at least some clearly flattened (at least basally); glochids yellow to tan or brown; flowers 4.5–7.5 cm long; sepaloids commonly greenish; petaloids yellow, bronze, pink, or violet; ovary usually spiny; fruit dry, tan to brown, spiny, 2.5–3 cm long, deciduous; seeds 4–6 mm long, whitish. Plants of this complex of morphologically differing forms intergrade freely among themselves, and they hybridize with the dry fruited *O. basilaris* var. *aurea*, *O. fragilis*, *O. nicholii*, and with the varieties of *O. polyacantha*. Further, they hybridize with the fleshy fruited *O. phaeacantha*, *O. littoralis*, and likely with *O. macrorhiza*. Intergradation with *O. polyacantha* is sufficiently complete as to pose the question of whether maintenance of the proposed segregates within separate species is reasonable. I follow tradition in maintaining them thusly, because, if a case is made for combining these two species, then a similiar case must be considered for union of all platyopuntias with which they intergrade into a single polymorphic species. The variants could then be recognized as belonging to numerous infraspecific taxa, approximately equal to the number of taxa recognized currently. Such a proposal would solve none of the basic problems resulting from intergradation of taxa, despite the convenience of having only one name at the specific level for all of the prickly pears. Three varieties are recognized.

1. Spines lacking in much of the joint, mainly confined to the upper half or along the upper edge; plants widespread .... *O. erinacea* var. *utahensis*

— Spines present in much or all of the joint; plants of the southern half of Utah 2

2(1). Spines stiff, rigid, the longest mainly 1–4 cm long; plants widespread in southern Utah .... *O. erinacea* var. *erinacea*

— Spines slender and more or less flexible, the longest 3–10 cm long; plants of Washington County .... *O. erinacea* var. *ursina*

Var. *erinacea* [*O. hystricina* sensu Utah authors]. Warm and mixed desert shrub communities at 885 to 1285 m in Beaver, Emery, Grand, Kane, Millard, San Juan, Washington, and Wayne counties; Nevada to Colorado, California, Arizona, and New Mexico; 20 (ix). It has been postulated (Benson 1982) that this phase of *O. erinacea* is one of the putative parents of *O. nicholii*, the other being *O. phaeacantha*. Along Glen Canyon there are many specimens which bridge this variety with *O. nicholii*.

Var. *ursina* (Weber) Parish [*O. ursina* Weber; *O. rubrifolia* Engelm. ex Coulter, type from St. George]. Warm desert shrub community at 760 to 900 m in Washington County; Nevada, California, and Arizona; 4 (ii). Our material shows evidence of mixing with var. *erinacea*.

Var. *utahensis* (Engelm.) L. Benson [*O. sphaerocarpa* var. *utahensis* Engelm; *O. rhodantha* K. Schum.; *O. xanthostemma* K. Schum.; *O. erinacea* var. *xanthostemma* (K. Schum.) L. Benson]. Blackbrush, pinyon-juniper, sagebrush, mountain brush, ponderosa pine, and aspen communities at 1220 to 2810 m in most if not all Utah counties; Idaho to California, Arizona, New Mexico, and Wyoming; 29 (xiii). This variety is the counterpart of *O. polyacantha* var. *polyacantha*, with which it hybridizes wherever they meet.

***Opuntia fragilis* (Nutt.) Haw.** [*Cactus fragilis* Nutt.; *O. fragilis* var. *denudata* Wiegand & Backeburg; *O. brachyarthra* Engelm. & Bigel.; *O. fragilis* var. *brachyarthra* (Engelm. & Bigel.) Coult.]. Plants mat forming, mainly 5–10 cm tall and to 5 dm wide; larger joints 2.5–7 cm long, 1–4 cm wide, obovate to ovate or orbicular to elliptic in outline, blue-green, often to half as thick as wide or more, readily detached and transported by animals; leaves caducous; areoles 3–12 mm apart; spines in most areoles or only in the upper ones or sometimes lacking, 1–9 per areole, disoriented, 4–25 mm long or more, terete to somewhat flattened; glochids tan to brown; flowers 3.5–6 cm long; sepaloids greenish; petaloids yellowish, greenish, bronze, or violet; fruit dry, tan, spiny or spineless, 1.2–2.5 cm long. This is a taxon of unusually great latitude of habitat types ranging from low elevation marshlands and riparian sites upwards to pinyon-juniper, ponderosa pine, sagebrush, mountain brush, and aspen communities at 1370 to 2565 m in Box Elder, Carbon, Duchesne, Emery, Garfield, Piute, San Juan, Sanpete, Sevier, Uintah, Utah, and Weber counties; British Columbia to Ontario, south to California, Nevada, Arizona, New Mexico, Texas, and Iowa; 18 (iii). Morphological amplitude of our specimens is greater than that reported for the species as a whole (Benson 1982), excluding hybrids presumably intermediate with both *O. erinacea* and *O. polyacantha*. Recognition of proposed infraspecific taxa seems moot.

***Opuntia littoralis* (Engelm.) Britt. & Rose** [*Opuntia engelmannii* var. *littoralis* Englem.]. Plants mainly 30–50 cm high and 0.5–1.2 m wide, more or less sprawling; larger joints 10–18 cm long, 7–14 cm wide, obovate to orbicular, green or glaucous; areoles mainly 15–30 mm apart; spines in all, or only in the upper, areoles, 1–6 per areole, mainly 2–7 cm long, spreading to deflexed, straight or curved, terete to somewhat flattened; glochids yellowish to brown; flowers 5–7.5 cm long; sepaloids greenish; petaloids yellow, the bases sometimes violet or rose-purple; fruit fleshy, reddish or purplish-red, armed with glochids, 3–6 cm long; seeds 3–6 mm long, tan or gray. Pinyon-juniper community (?) in Washington and San Juan counties (reported by Benson 1982); Nevada, California, and Arizona; 1 (0). This plant can be mistaken for *O. phaeacantha*, with which it is at least partially sympatric. Our material is assigned to **var. *martiniana* (L. Benson) L. Benson** [*O. eriocentra* var. *martiniana* L. Benson].

Opuntia macrorhiza **Engelm.** [*O. utahensis* J. A. Purpus; *O. compressa* Macbr.]. Plants mainly 7–15 cm high and 2–15 dm wide or more; larger joints 5–12 cm long, 5–7.5 cm wide, obovate to orbicular, glaucous; leaves caducous; spines mainly in upper areoles, 1–6 per areole, commonly deflexed, straight or slightly curved, 1.5–5 cm long, terete or somewhat flattened; glochids yellow to brown; flowers 5–6.5 cm long; sepaloids greenish or reddish; petaloids yellow or tinged reddish basally; ovary smooth at anthesis, with few areoles; fruit fleshy, purple or purplish, with some glochids, 2.5–5 cm long; seeds 4–5 mm long, tan or gray. Pinyon-juniper and mountain brush communities in Garfield, Kane, Salt Lake, San Juan, and Washington counties, the reports mainly by Benson (1982); Idaho to Wisconsin, south to Mexico, Texas, and Louisiana; 3 (0). This is mainly a plains species, with extensions into Utah where some of the reports might represent recent introductions. The similar *O. humifusa* (Raf.) Raf. is reported for Utah on the basis of a collection from Utah County (Mason 6570 US), which was taken from along a railroad right-of-way. It is distinguished by having green joints and spines 1 per areole.

Opuntia nicholii **L. Benson.** Plants mainly 15–25 cm high and 0.5–2 m wide or more; larger joints 10–20 cm long and 5–12 cm wide, narrowly obovate to obovate, bluish-green; areoles 10–20 mm apart; spines usually in all areoles, 4–7 per areole, deflexed, often twisted and curving, mainly 5–12 cm long, flattened, some more than 1 mm thick; glochids yellow or tan; flowers 6–7 (8) cm long; sepaloids green, edged with purple or yellow; petaloids violet or yellow; fruit dry, tan to brown, 2.5–3.5 cm long, more or less spiny; seeds 7–8 mm long, whitish. Salt desert shrub and warm desert shrub communities at 1200 to 1500 m in Garfield, Kane, and San Juan counties (where it grows along Glen Canyon); Arizona; a Plateau endemic; 2 (i). Evident intermediates between *O. nicholii* and both *O. erinacea* var. *erinacea* and *O. phaeacantha* are known. Benson (1982) postulates a hybrid origin for this entity, and states that it should probably best be treated at varietal rank, but with which species?

Opuntia phaeacantha **Engelm.** Plants 30–90 cm high and 3–15 dm wide or more; larger joints 10–40 cm long, 7–25 cm wide, obovate to suborbicular, bluish green; areoles mainly 20–34 mm apart; spines in most areoles or restricted to upper ones or along the margin, or none, 1–9 per areole, spreading or deflexed, 2–8 cm long, flattened at least basally in some; glochids brown, reddish, or tan; flowers 6–7.5 cm long; sepaloids greenish, edged yellow or red; petaloids yellow, or suffused with red below; ovary spineless, but with glochids; fruit fleshy, purple to red-purple, 3.5–8 cm long; seeds 4–5 mm long, tan to gray. Three intergrading varieties have been identified from Utah (Benson 1982); their recognition at taxonomic rank is questionable, at least as far as our specimens are concerned.

1. Larger joints 10–15 cm long and 7–10 cm wide; plants of Washington and San Juan counties .... *O. phaeacantha* var. *phaeacantha*
— Larger joints 12–40 cm long and 9–25 cm wide; plants of various distribution 2
2(1). Joints mainly 12–20 cm long and 9–15 cm wide; plants rather broadly distributed in southern Utah .... *O. phaeacantha* var. *major*
— Joints mainly 20–40 cm long and 15–25 cm wide; plants of San Juan and Washington counties .... *O. phaeacantha* var. *discata*

Var. *discata* (Griffiths) Benson & Walkington [*O. discata* Griffiths]. Warm desert shrub, pinyon-juniper, and sagebrush communities at 905 to 1800 m in San Juan (White Canyon, associated with prehistoric Indian dwellings) and Washington counties; California to Texas and Mexico; 3 (ii).

Var. *major* Engelm. Warm desert shrub, pinyon-juniper, and mountain brush communities in Garfield, Kane, San Juan, and Washington counties; Nevada to Kansas, south to California, Mexico, and Texas; 12 (iii). This is the common phase of the species in Utah; plants north of the southern tier of counties having fleshy fruit probably belong to *O. macrorhiza*, with which transitional forms are known.

Var. *phaeacantha*. This variety is reported by Benson (1982) from Washington County; Arizona, Colorado, New Mexico, Texas, and Mexico; 0 (0).

Opuntia polyacantha Haw. Plants mainly 5–20 cm high and 3–30 dm wide or more; larger joints 5–15 (20) cm long (rarely longer) and 4–12 cm wide, obovate to orbicular, bluish green, not readily detached; areoles mainly 5–15 mm apart; spines variously borne in some or all areoles or lacking, often 6–10 per areole, variously oriented (all erect or spreading or some or all deflexed), straight or curved, terete (or somewhat flattened); glochids yellowish or tan; flowers 5–8 cm long; sepaloids green, margined with yellow or red; petaloids yellow, bronze, or pink to violet; ovary with glochids and often with spines; fruit dry, 2–4 cm long, spiny, tan or brownish, deciduous; seeds 3–6 mm long, tan to white. This species, along with *O. erinacea*, forms a plexus around which revolve all other species of subgenus Opuntia (the platyopuntias) in Utah. Members of this complex form hybrids with *O. fragilis*, *O. erinacea*, *O. basilaris*, and *O. phaeacantha*. Those, in turn, are transitional to all other species. Diversity of form and joint size; spine length, number, size, cross-sectional shape, and color; flower size and color; and other features give indications of genetic variability, differential response to ecological situations, and of problems of interpretation. Four varieties from Utah are treated by Benson (1982); they are more or less sympatric and intergrading.

1. Spines slender, flexible and curving, often whitish; plants of Grand and San Juan counties .... *O. polyacantha* var. *trichophora*

— Spines slender to coarse, not flexible (penetrating the skin before collapsing), mostly straight, or sometimes lacking; plants of various distribution 2

2(1). Spines mainly in upper areoles; fruits sparingly spiny; plants mainly of the eastern tier of counties .... *O. polyacantha* var. *juniperina*

— Spines in most areoles, or if less abundant or lacking in the lower ones then often of other distribution; fruits often spiny 3

3(2). Spines in lower areoles mainly less than 12 mm long, those of upper areoles mainly less than 4 cm long, or spines lacking .... *O. polyacantha* var. *polyacantha*

— Spines in lower areoles mainly over 12 mm long, those of upper areoles often over 4 cm long .... *O. polyacantha* var. *rufispina*

Var. *juniperina* (Britt. & Rose) L. Benson [*O. juniperina* Britt. & Rose]. Desert shrub and pinyon-juniper communities at ca 1400 to 2000 m in Grand, San Juan, and Uintah counties; Wyoming to Colorado, New Mexico, and Arizona; 3 (i). As far as specimens from Utah are concerned this taxon could pass under var. *polyacantha* without adding much to the variation of the expanded typical variety. The coarser spines in fewer upper areoles have been considered as definitive.

Var. *polyacantha* [*O. polyacantha* var. *watsonii* Coult., type presumably from Summit County]. Salt Desert shrub, mixed desert shrub, pinyon-juniper, sagebrush, mountain brush, mixed conifer, and aspen communities at 1370 to 2565 m in probably all Utah counties; British Columbia to Saskatchewan, south to Nevada, New Mexico, and Oklahoma; 36 (iv). This variety is transitional with the former and the next.

Var. *rufispina* (Engelm. & Bigel.) L. Benson [*O. missouriensis* var. *rufispina* Engelm. & Bigel.]. Blackbrush, mixed desert shrub, and pinyon-juniper communities at 1370 to 2200 m in Carbon, Emery, Garfield, Grand, Kane, Millard, San Juan, Washington, and Wayne counties; Wyoming to Nevada and California, south to Arizona and Texas; 21 (iii). This assemblage seems not to represent plants with genetic affinities. Rather the specimens appear to be artificial aggregations of phenotypically similar individuals. The use of spine characteristics as diagnostic results in a dilemma; the assemblage thus defined should be allied genetically to be recognized at a taxonomic level, but the definition is faulty. Thus, those plants of the Colorado drainage system show evidence of derivation from hybridization with *O. erinacea;* the plants of the Great Basin do not.

Var. *trichophora* (Engelm. & Bigel.) Coult. [*O. missouriensis* var. *trichophora* Engelm. & Bigel.]. Desert shrub and pinyon-juniper communities at 1125 to 1250 m in Grand, Kane, and San Juan counties; Colorado, Arizona, and New Mexico, Oklahoma, and Texas; 6 (iv).

***Opuntia pulchella* Engelm.** Sand Cholla. Plants mainly 3–10 cm tall and about as broad, arising from an areolate glochid-armed tuberous joint 2–7 cm thick or more; joints mainly 1–5 cm long and 0.6–1.5 (2) cm thick, clavate to cylindric, green or blue-green; tubercles 5–9 mm long and 4–5 mm wide; areoles spineless or with the upper mainly spiniferous, 8–15 per areole, straight or curved, 1–3.5 cm long or more, strongly flattened, the epidermal sheath not at all or poorly developed; glochids yellow to brown; flowers 3–4.5 cm long; sepaloids green, margined with pink-purple; petaloids purple to violet; fruit 2–3 cm long, fleshy, red, prominently areolate and spiny; seeds 3–4.5 mm long, whitish. Salt and mixed desert shrub communities at 1430 to 1770 m in Juab, Millard, and Tooele counties; Nevada; a Great Basin endemic; 8 (iv). This taxon was named three times from Utah, all of the names based on types taken from the Desert Experimental Range in western Millard County, i.e., *Micropuntia brachyropalia* Daston, *M. barkleyana* Daston, and *M. spectatissima* Daston. All are characteristic of the species as it occurs in Utah, and none are worthy of taxonomic consideration.

***Opuntia whipplei* Engelm. & Bigel.** Plants low shrubs or less commonly mat-forming, mainly 10–60 cm tall or more; larger joints 2–15 cm long and 1–2 (2.5) cm thick; tubercles 8–9 mm long, 3–5 mm wide; leaves caducous; spines 4–10 or more per areole, straight, mainly 0.6–3 cm long, subulate to flattened; glochids yellow to tan or whitish; flowers 2–4 cm long; sepaloids and petaloids yellowish or yellowish green; fruit fleshy, 2–3 cm long, yellow, glochidiate; seeds 2.5–3 mm long, tan. Desert shrub-grass and pinyon-juniper communities at 1340 to 1895 m in Beaver, Iron, Kane, Millard, and Washington counties; Nevada, Colorado, Arizona, and New Mexico; 15 (x). Our material belongs to var. ***whipplei*.** Specimens with short terminal joints have been regarded tentatively as var. *multigeniculata*, but they fit in a graded series with *O. whipplei* in a strict sense. Dwarf plants at the limits of their ecological tolerance seem to represent a "cactus-line," corresponding to the dwarf conifers at "timberline." This seems to be the case with *O. whipplei* at the northern margin of its distribution in southwestern Millard County. A taxon represents the sum of its characteristics, not merely those considered to be diagnostic. *O. multigeniculata* Clokey is evidently restricted to the Spring (Charleston) Mountains and vicinity in southern Nevada.

PEDIOCACTUS Britt. & Rose

Plants globose to depressed-hemispheric, solitary; tubercles spirally arranged; areoles woolly, at least when young, with spines various but not hooked; flowers subterminal, borne at one side of the areole at the tubercle apex, small; sepaloids shorter than the petaloids; fruit dry, green, becoming tan to brownish or yellowish, naked or scaly, dehiscing by a vertical slit; seeds black tuberculate.

HEIL, K., B. ARMSTRONG, AND D. SCHLESER. 1981. A review of the genus *Pediocactus*. Cactus & Succ. J. (U.S.) 53: 17–39.

1. Central spines 1–7, 6–30 mm long or more 2
— Central spines lacking, the longest lateral spines mainly less than 6 mm long 3

2(1). Longest spines mainly 12–25 mm long; sepaloids long-fimbriate; plants known only from gypsiferous substrates in Washington and Kane counties .... *P. sileri*
— Longest spines mainly 6–12 mm long; sepaloids subentire or shortly fimbriate; plants broadly distributed, seldom as above .... *P. simpsonii*

3(1). Longest spines 4 mm long or less, white, or lacking, often obscured by a dense mat of persistent white hairs; flowers peach to pink; plants of western Wayne County .... *P. winkleri*

Longest spines more than 4 mm long, pale yellowish, not obscured by hairs, the woolly hairs pale yellowish and caducous; flowers yellow to bronze or peach; plants of north central Emery County .... *P. despainii*

Pediocactus despainii **Welsh & Goodrich** Plants solitary or less commonly colonial, subglobose to depressed-hemispheric, 3.8–6 cm tall, 3–9.5 cm wide; tubercles 6–10 mm long, 5–11 mm wide; areoles elliptic, persistently white-woolly, the central spines lacking; radial spines 9–13, 1.7–6 mm long, pale yellowish; flowers 1.5–2.5 cm long, 1.8–2.5 cm wide; petaloids yellow-bronze to bronze or pinkish; fruit green, drying reddish brown, smooth, obovoid, 9–11 mm long, 10–12 mm wide; seeds shiny black, papillate to ridged, 3–3.5 mm long. Open pinyon-juniper community on limestone gravels at ca 1830 m in Emery County; endemic; 5 (0).

Pediocactus sileri **(Engelm.) L. Benson** Gypsum Cactus. [*Echinocactus sileri* Engelm. in Coult.; *Utahia sileri* (Engelm.) Britt. & Rose]. Plants solitary (less commonly colonial), depressed-hemispheric to cylindroid, 5–25 cm high, 6–12 cm wide; tubercles 9–15 mm long, 6–11 mm wide; areoles circular, persistently white-woolly; central spines 3–7, 13–30 mm long, blackish brown when young, straight; radial spines 11–15, 11–21 mm long, white; flowers 18–22 mm long, 20–30 mm wide; petaloids yellow or yellowish with purple veins; sepaloids conspicuously fringed; fruit dry, greenish yellow, 1.2–1.5 cm long; seeds gray to black, 3.5–5 mm long. Salt desert shrub community at ca 900 to 1590 m in Kane and Washington counties; Arizona; a Plateau endemic; 1 (i). The type locality for this remarkable species is Pipe Springs, Arizona, but those springs were thought by early collectors to be in Utah, hence the name *Utahia*, which commemorates an Arizona type.

Pediocactus simpsonii **(Engelm.) Britt. & Rose** [*Echinocactus simpsonii* Engelm.; *P. hermannii* W. T. Marshall, type from near Hatch; *E. simpsonii* var. *minor* Engelm.; *P. simpsonii* var. *minor* (Engelm.) Cockerell]. Stems solitary or colonial, depressed-hemispheric to subglobose, 2–15 cm high, 3–20 cm wide (or more); tubercles 5–25 mm long, 4–7 mm wide; areoles elliptic to subcircular; central spines (1–3) 4–10, mainly 5–25 mm long, brownish or blackish; radial spines mainly 10–25, white; flowers 1.2–3 cm long; petaloids whitish, pinkish, yellowish or greenish; sepaloids shortly fimbriate; fruit green, often turning reddish brown, with few scales, 6–11 mm long, 5–10 mm wide; seeds gray to black, tuberculate, 2–3 mm long. Shadscale, mixed desert shrub, pinyon-juniper, sagebrush, and Douglas fir communities at 1460 to 2830 m in Beaver, Box Elder, Carbon, Duchesne, Emery, Garfield, Grand, Juab, Piute, San Juan, Sevier, Tooele, Utah, Washington, and Wayne counties; Washington to Wyoming, south to Nevada, Arizona, and New Mexico; 26 (viii). Segregation of this common species of cactus into varieties seems not to be practical or even possible for Utah materials. Ridge tops in some south central mountains and plateaus support one to several plants per square foot, mainly flush with the ground surface.

Pediocactus winkleri **Heil.** Plants solitary or sometimes colonial, 3.9–6.8 cm tall, 2.7–5 cm wide; tubercles 4–7 mm long, 5–7 mm wide; areoles elliptic, persistently white-woolly; central spines lacking; radial spines 8–14, 1.5–4 mm long, white; flowers 1.7–2.2 cm long, 1.7–3 cm wide; petaloids peach to pink; sepaloids like the petaloids, except the outer darker; fruit green, drying reddish brown, smooth, obovoid, 7–10 mm long, 8–11 mm wide; seeds shiny black, papillate to ribbed, 2.5–3 mm long. Salt desert shrub communities at 1460 to 1590 m in Wayne Co.; endemic; 5 (0). This is a remarkable tiny plant of poor quality, saline, fine-textured substrates.

Sclerocactus Britt. & Rose

Plants subglobose, depressed-hemispheric, ovoid, obovoid, or cylindroid; ribs 8–17; tubercles coalescent; areoles circular to elliptic; central spines 0 or 1–10, usually 1 or more hooked, or all straight; radial spines 2–15, straight; flowers subterminal, borne on upper side of tubercle adjacent to the areole, the scar persisting; floral tube short; petaloids pink to violet, white, or yellow; fruit dry, green turning reddish to tan, naked or with scales, dehiscent by basal and horizontal or lateral and vertical slits; seeds black, papillate-reticulate. NOTE: The taxonomy of this genus is subject to interpretation because of the remarkable diversity of form present in each of the species complexes.

1. Plants depressed-hemispheric to subglobose; areoles retaining juvenile pubescent radial spines for some years, finally with 1 or 2 hooked central spines; plants of the Great Basin .... *S. pubispinus*

— Plants variously shaped, but if as above and with areoles retaining juvenile radial spines for several years, then the spines glabrous and plants not of the Great Basin 2

2(1). Flowers mostly 2–3 cm long and broad; yellowish, pink, or white with pale pink midrib dorsally; juvenile condition retained for several years; plants of Emery and Wayne counties .... *S. wrightiae*

— Flowers mostly 3.5–5 cm long and broad, rose pink to violet, white, or yellow; plants of broad distribution in eastern Utah .... *S. whipplei*

Sclerocactus pubispinus **(Engelm.) L. Benson** [*Echinocactus pubispinus* Engelm.]. Plants solitary or sometimes colonial, depressed-hemispheric to ovoid, 1–10 cm high, 2–15 cm wide; ribs 6–13; tubercles more or less developed; areoles circular to elliptic; juvenile spines and often the others (in part) densely or sparingly white-pubescent, finally glabrate; central spines lacking or 1–5, the lower one often hooked, 1–3 cm long, the upper one flattened, 5–35 mm long, 0.7–2.2 mm wide; radial spines 5–12, spreading; flowers 2.5–3.5 cm long; sepaloids bronze to brownish; petaloids yellow, bronze, pink, or violet to rose-purple; fruit dry, green or pink becoming tan to brownish, ellipsoid to obovoid, opening by vertical slits; seeds 2.8–3.4 mm long, papillate, black. This species was named simultaneously in 1863 as *Echinocactus pubispinus* and as *E. whipplei* var. *spinosior*. The type of the former was taken in Pleasant Valley, Juab County, Utah, or in adjacent White Pine County, Nevada (the boundary bisects the valley), and that of the latter was taken in the Dugway or Thomas ranges in central northern Juab County. Both remained obscure for almost a century, with *S. pubispinus* being ignored and var. *spinosior* being placed with *S. whipplei* and interpreted as including what now belongs in var. *intermedius* of that species (sensu stricto, which it resembles in its broad upper central spines). The type of *S. pubispinus* is a juvenile plant lacking both flowers and fruit; that of var. *spinosior* consists of flowers and seeds. Modern interpretations are based on interpolations of presumed collection localities with known modern occurrences of these dwarf cacti. In a way these peculiar cacti share characteristics of *S. polyancistrus* (Engelm. & Bigel.) Britt. & Rose of southern Nevada (pubescent spines and the tendency to flattened upper central spine) and with *S. whipplei* (the flattened upper central spine). The smaller flowers and depressed growth form are diagnostic from both. There are two intergrading and partially sympatric varieties present.

1. Flowers rose to violet; widest upper central spines 1–2.2 mm wide .... *S. pubispinus* var. *spinosior*

Flowers bronze to yellow; widest upper central spines 0.7–1 mm wide .... *S. pubispinus* var. *pubispinus*

Var. ***pubispinus*** Shadscale, sagebrush, winterfat, rabbitbrush, and pinyon-juniper communities on calcareous and dolomitic gravels and outcrops at 1800 to 1955 m in Beaver, Box Elder, Iron, Juab, Millard, and Tooele counties; Nevada; a Great Basin endemic; 13 (vi).

Var. ***spinosior*** **(Engelm.) Welsh comb. nov.** [based on: *Echinocactus whipplei* var. *spinosior* Engelm. Trans. Acad. Sci. St. Louis 2: 199. 1863; *S. spinosior* (Engelm.) Woodruff & Benson]. Shadscale, rabbitbrush, sagebrush, and pinyon-juniper communities on calcareous and igneous gravels and clay silts at

1525 to 1985 m in Beaver, Juab, Millard, and Sevier counties; Arizona (?); 15 (xi). The range of this variety is partially sympatric with var. *pubispinus* in western Beaver County and intermediates are known. The population from Sevier County differs in subtle ways from the remainder of the taxon, but does not seem to be worthy of taxonomic rank.

Sclerocactus whipplei **(Engelm.) Britt. & Rose** [*Echinocactus whipplei* Engelm. & Bigel.]. Plants solitary or in small colonies, depressed-hemispheric, obovoid, ovoid, or cylindric, 5–35 cm tall or more, 5–15 cm thick; ribs mainly 8–15, tuberculate; central spines 1–4, the lower one (sometimes 2–4) hooked or all straight, mainly 1–7.5 cm long, curved or some or all of them straight, the upper central spine (at least) usually pale and flattened to flat and ribbonlike, 1–5 cm long or more, 0.7–3.5 mm wide, erect; radial spines 7–12 or more; flowers 3.5–5 cm long; sepaloids greenish, margined with rose purple, pink, white, or yellow; petaloids pink, violet, white, or yellow; fruit dry, green, becoming tan, sparingly scaly, 1.2–2.5 cm long; seeds 2–3.4 mm long, black, papillate. Two intergrading varieties are recognizable among our Utah materials.

1. Central spines all straight or essentially so; plants commonly of terrace gravels at lower elevations in the Uinta Basin and rarely elsewhere .... S. *whipplei* var. *glaucus*

Central spines hooked, at least the lowermost; plants of broad distribution, transitional to the above in the Uinta Basin .... S. *whipplei* var. *roseus*

Var. *glaucus* (J. A. Purpus) Welsh comb. nov. [based on: *Echinocactus glaucus* J. A. Purpus ex K. Schum. Gesamtb. Kakteen. 438. 1898]. Salt desert shrub and shrub-grass communities on terrace gravels and less commonly on clays of the Uinta Formation at ca 1430 to 1770 m in Duchesne and Uintah (and San Juan?) counties; Colorado; 17 (ix). Plants with straight spines have long been known, and have been recognized as belonging to this genus. Their status has been open to question, because they differ in no other discernible way from the body of the species. Also, there is a question as to whether all of the straight-spined plants in Utah (e. g., Welsh et al. 21187 BRY) and in central western Colorado constitute "a taxon." Instead, could they not be merely similarly derived evolutionary end lines arrived at quite independently? The intergradation of the Utah materials with the species suggests such a derivation, and the Uinta Basin material might be more closely allied to the adjacent populations with hooked spines than to those in Colorado with straight spines. Possibly they are not more important taxonomically than spineless phases of other plants scattered through spined taxa elsewhere in the Cactaceae. A peculiar phase from the Pariette Draw region of southeastern Duchesne County has a long juvenile stage, with the initial central spines very short (to 2 mm long) and hooked or straight. It does not seem to warrant taxonomic recognition.

Var. *roseus* (Clover) L. Benson [*S. havasupaiensis* var. *roseus* Clover; *S. intermedius* Peebles, type from Pipe Springs, Arizona; *S. whipplei* var. *intermedius* (Peebles) L. Benson; *S. parviflorus* var. *intermedius* (Peebles) Woodruff & Benson; *S. parviflorus* Clover & Jotter, type from Forbidding Canyon; *S. contortus* Heil, type from eastern Wayne County; *S. terrae-canyonae* Heil, type from Trachyte Wash]. Some tiny juvenile plants have pubescent spines, but the juvenile stage is apparently arrested in most portions of this variety. Salt and mixed desert shrub, pinyon-juniper, sagebrush, and ponderosa pine communities at 1125 to 2440 m in Carbon, Duchesne, Emery, Garfield, Grand, San Juan, Sevier, Uintah, and Wayne counties; Colorado, New Mexico, Arizona, and Nevada; 102 (xiv). This variety is almost as variable as the species itself. It has been treated previously at specific rank (as three separate species) and as consisting of two varieties. With the degree of variability exhibited, it is not surprising that so many divergent views should have developed; it is surprising that even more segregation was not attempted. *S. contortus* is a slender-spined phase in which the spines are contorted, a condition that seems to be unworthy of consideration from a taxonomic standpoint. S. *terrae-canyonae* appears to be more substantially based, with its long slender spines and yellow flowers. There is little correlation, however, between flower color and spine length. Long-spined phases are more common in the southeastern portion of Utah, but the flowers of the long-spined phases are mainly pink to violet. The var. *intermedius* is more difficult to discount. In the extreme situations that variety has the uppermost central spine flattened and ribbonlike, commonly 1–3.5 mm wide at the base, with var. *roseus* (or S. *parviflorus* per se) having the uppermost spine merely flattened and mainly 0.7–1 mm wide. There are as many intermediates as there are extremes, and, until other diagnostic criteria are identified, it seems best to include all of the tremendous range of variation within an expanded var. *roseus* of S. *whipplei*.

Sclerocactus wrightiae **L. Benson.** Plants depressed-hemispheric to obovoid or short-cylindric, mainly 6–12 cm long and 4–8 cm thick; ribs mostly 8–13; tubercles more or less developed; areoles circular to elliptic; juvenile spines glabrous; central spines 1–4, the lower one often hooked on at least the upper tubercles, mostly 10–20 mm long, the uppermost 1–2.5 cm long, flattened, 0.8–1.5 mm wide; radial spines 8–11, spreading; flowers 2–3.5 cm long; sepaloids green or variously tinged with red or brown; petaloids yellowish to white or pink; fruit ellipsoid, 9–12 mm long; seeds black, tuberculate, 3–3.5 mm long. Salt desert shrub and shrub-grass to juniper communities at 1460 to 1865 m on Mancos Shale (Bluegate, Tununk, Emery, and Ferron members), Dakota, Morrison, Summerville, and Entrada formations in Emery and Wayne counties; endemic; 14 (iii). The small flowers and short spines are evidently diagnostic. Occasional intermediates with S. *whipplei* var. *roseus* occur in Emery County near the Sevier County line—at edaphic ecotones marking the boundary between shale and sandstone members of the Mancos Shale Formation.

AUTUMN AND WINTER FOOD HABITS OF BOBCATS IN WASHINGTON STATE[1]

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Abstract.— The stomach contents were examined from 324 western Washington bobcats (*Felis rufus*) and 123 from eastern Washington taken by hunters from 1976 through 1980, for major prey items as well as sex- and age-related differences in diet. Western Washington bobcats ate primarily mountain beavers (*Aplodontia rufa*) (42% occurrence) and snowshoe hares (*Lepus americanus*) (26%). Within that population females ate larger quantities of smaller prey such as douglas squirrels (*Tamiasciurus douglasi*) and lesser amounts of deer (*Odocoileus* sp.) than males. Bobcat diets in eastern Washington were more diverse; main foods consisted of lagomorphs (*Sylvilagus nuttallii, Lepus* sp.) (20%), red squirrels (*Tamiasciurus hudsonicus*) (15%), deer (11%), and voles (*Microtus* sp.) (11%). Age-related differences were most prevalent in this population, with adults consuming larger quantities of deer and larger prey than did kittens.

Food habits, the most widely studied aspect of bobcat (*Felis rufus*) biology, are known for most of the range for this species. Earlier studies of bobcat food habits were concerned primarily with prey identification and the impact of predation on game species (Marston 1942, Pollack 1951, Erickson 1955, Progulske 1955, Gashwiler et al. 1960, Petraborg and Gunvalson 1962). Only recently have investigators considered differences in diet related to sex and age (Fritts and Sealander 1978, Toweill 1983). Differential exploitation of prey resources should benefit species such as the bobcat, in which there is sexual dimorphism in body size (Selander 1966) and the female raises the young alone (Ewer 1968). Age-related differences in diet also may occur in young solitary carnivores whose hunting capabilities may not be fully developed.

This paper reports bobcat food habits in Washington state from 1976 through 1980. Important prey items, as well as differences in diet related to sex and age, are discussed. Two geographically distinct populations with separate faunas occur in the state: *Felis (Lynx) rufus fasciatus* occurs west of the Cascade Mountain crest (western Washington) and *F. r. pallescens* is found east of this divide (eastern Washington) (Hall and Kelson 1959).

Methods

Bobcat carcasses were collected from hunters by Washington Department of Game personnel between October and March (legal hunting seasons) from 1976 through 1979 in western Washington, and from 1976 through 1980 in eastern Washington. Stomach contents were washed in a fine mesh sieve, drained and separated (Korschgen 1971). Food items were identified to genus, and to species when possible, by diagnostic bones or hair, or in a few cases by hair impression (Moore et al. 1974). Percent occurrence (number of occurrences of a species/total number of stomachs × 100) and relative weight (total weight of a species/total weight of all species × 100) were determined for each food item.

Bobcat ages were determined by counting cementum annuli in the canine root tip (Crowe 1972). Bobcats with an open root canal or lacking permanent dentition were aged as kittens (<1 year old) (Crowe 1975); other age categories were yearling (1–2 years old) and adult ($\geq 2\frac{1}{2}$ years old).

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Western and eastern Washington populations were treated separately in the analyses of specific food items but were compared with respect to total stomach content weights and number of empty stomachs. The relative weights of food items were analyzed with two-way multivariate analyses of variance (ANOV) (Morrison 1976). This multivariate investigation of sex and age effects was supplemented by univariate ANOV on relative weight and percent occurrence of each food item and by using Fisher's protected lsd procedure (Steele and Torrie 1980) where necessary to determine pairwise differences. Because of the large variation involved, we used a significance level of $p<0.10$. We combined data across years within populations since there was no variation in proportions.

RESULTS

Mountain beavers (*Aplodontia rufa*) and snowshoe hares (*Lepus americanus*) were the primary food items found in 324 western Washington bobcat stomachs (Table 1); together they occurred in 68% of the stomachs and constituted 83% of the total prey weight consumed. Mammalian prey were found in 96% of the nonempty western Washington stomachs and accounted for 98% of the total prey weight consumed.

Food habits of eastern Washington bobcats were more diverse than bobcats in western Washington (Table 2). The primary food items were lagomorphs (*Sylvilagus nuttallii*, *Lepus townsendii*, and *L. californicus*), red squirrels (*Tamiasciurus hudsonicus*), deer (*Odocoileus hemionus* and *O. virginianus*), and *Microtus* sp. These four prey categories were found in 57% of the eastern Washington bobcat stomachs and composed 73% of the total prey weight. Mammals were eaten 80% of the time and accounted for 85% of the prey weight consumed.

Stomachs of eastern Washington bobcats were empty more often than western Washington specimens ($p<0.10$); the average weight of stomach contents in eastern Washington (empty stomachs excluded) was less than that of western Washington bobcats ($p<0.02$) (Table 3). In western Washington, the average weight of stomach contents of males was greater than for females ($p<0.004$). Stomach content weights differed between adults and kittens ($p<0.07$); no difference was found between yearlings and adults or kittens. In eastern Washington, no significant age or sex differences were found in average stomach content weights. We obtained these same results for both populations when all stomachs (empty and nonempty) were considered.

For western Washington bobcats, the relative weight of prey remains differed between male ($n=174$) and female ($n=139$) bobcats ($p<0.02$). Thus, male stomachs averaged 7.1 ± 25.2 g ($\bar{x}$ ± SD) of deer and 5.1 ± 20.9 g of other mammals compared to 1.0 ± 6.8 g and 0.7 ± 8.5 g for females, respectively ($p<0.008$; 0.03); female stomachs averaged 9.3 ± 27.8 g of douglas squirrels (*Tamiasciurus douglasi*) compared to 4.6 ± 19.2 g for males ($p<0.07$). Although there were no

TABLE 1. Stomach contents of 324 western Washington bobcats collected from 1976 through 1979.

	Percent occurrence	Relative weight (%)
MAMMALS		
Aplodontia rufa	42	50
Lepus americanus	26	33
Tamiasciurus douglasi	10	3
Odocoileus sp.	7	7
Microtus sp.[a]	4	1
Glaucomys sabrinus	1	1
Castor canadensis	1	1
Sorex sp.[b]	1	tr[c]
Felis rufus	1	3
Ondatra zibethica	1	tr
Cervus canadensis	tr	tr
Peromyscus maniculatus	tr	tr
Erethizon dorsatum	tr	tr
Scapanus orarius	tr	tr
Unidentified mammal	2	tr
Total	96	98
BIRDS		
Troglodytes troglodytes	3	tr
Melospiza melodia	1	tr
Pipilo erythrophthalmus	1	tr
Ixoreus naevius	1	tr
Scolopacidae	tr	tr
Tetraonidae	tr	1
Unidentified bird	tr	tr
Total	7	1
SALMONID	2	1
VEGETATION	3	tr
EMPTY	17	—

[a] Includes *Microtus oregoni*, *Clethrionomys* sp.
[b] Includes *Sorex vagrans*, *S. trowbridgii*.
[c] tr = items occurring ≤ 0.5%.

overall age differences in food habits, the relative weight of squirrel remains in 76 kitten stomachs averaged 11.4 ± 30.9 g compared to 3.9 ± 17.6 g in 139 adults ($p<0.05$).

In western Washington, birds occurred more often ($p<0.07$) in 67 adult (6%) and kitten females (10%) than 72 adult males (0%), and 9% of the 57 yearling males had eaten birds compared to 2% of the 41 yearling females.

There was a slight difference in the eastern Washington population among the 49 kittens, 17 yearlings, and 48 adults when the relative weights of all prey remains were examined simultaneously ($p<0.09$). Analyses of individual prey items showed that adults averaged 17.7 ± 37.8 g of deer compared to 9.0 ± 19.2 g in kitten ($p<0.05$) and 6.8 ± 24.4 g in yearling ($p<0.10$) stomachs. Also, kittens had consumed an average of 19.3 ± 38.7 g of mice compared to 1.9 ± 8.1 g for yearlings ($p<0.09$). Sixty-five female bobcats had consumed an average of 15.0 ± 33.0 g of red squirrels compared to 8.6 ± 27.9 g for males (n + 49) ($p<0.05$) in the only sex-related dietary difference in the eastern Washington population.

TABLE 2. Stomach contents of 123 eastern Washington bobcats collected from 1976 through 1980.

	Percent occurrence	Relative weight (%)
MAMMALS		
Lagomorphs[a]	20	32
Tamiasciurus hudsonicus	15	14
Odcoileus sp.	11	21
Microtus sp.[b]	11	6
Peromyscus maniculatus	6	1
Neotoma cinerea	2	2
Glaucomys sabrinus	2	2
Eutamius sp.	2	tr[c]
Erethrizon dorsatum	2	1
Ondatra zibethica	2	3
Marmota sp.	2	1
Citellus sp.	1	1
Castor canadensis	1	2
Sciurus griseus	1	1
Perognathus parvus	1	tr
Unidentified mammal	3	tr
Total	80	85
BIRDS		
Tetraonidae	5	9
Fringillidae	1	tr
Spinus pinus	1	tr
Agelaius phoeniceus	1	tr
Anas platyrhynchos	1	1
Domestic chicken	1	4
Unidentified bird	5	1
Total	15	15
VEGETATION	5	tr
EMPTY	26	—

[a] Includes *Sylvilagus nuttallii, Lepus townsendii, L. californicus.*
[b] Includes *Microtus pennsylvanicus, M. montanus, M. longicaudus.*
[c] tr = items occurring ≤ 0.5%.

Ten percent of the bobcat kittens in eastern Washington had eaten mammals compared to 24% of the yearlings and 19% of the adults ($p<0.09$). Squirrels occurred in 20% of the female stomachs and 10% of the males ($p<0.10$). Deer remains were found in 16% of the 31 adult and 20% of the 10 yearling females compared to 8% of the 24 kitten females; 24% of the 17 adult males had eaten deer, but none of the 25 kitten or 7 yearling males had ($p<0.10$).

DISCUSSION

Mountain beavers were the most important bobcat prey in western Washington. Schwartz and Mitchell (1945) found mountain beavers in only 1.3% of 6 bobcat stomachs and 99 feces examined from northwestern Washington. Nussbaum and Maser (1975) reported mountain beavers in 1.6% and 5.3% of bobcat feces (n=34, 143) from two ranges in western Oregon. Although comparative mountain beaver densities were not indicated in Schwartz and Mitchell's study, the increased use by bobcats in Washington may be a function of mountain beaver availability. Logging and burning in western Washington have increased the proportion of forests in early successional stages (Franklin and Dyrness 1973), providing better habitat for mountain beavers. Mountain beaver densities may have increased with this habitat change and provided a more abundant food resource for bobcats than in previous years.

Evidence of bobcats killing deer has been well documented (Young 1958, Marston 1942, Erickson 1955, McCord 1974). Equal occurrences of deer in the stomachs of all bobcat age classes in western Washington suggests carrion utilization. The greater occurrence of deer in adult diets in eastern Washington indicates either greater carrion use or a higher incidence of predation by more capable hunters.

The higher proportion of empty stomachs and smaller average stomach content weights for eastern Washington bobcats compared to western Washington specimens may indicate a lower prey base available to eastern Washington bobcats. There was no kitten survival to the winter population on one study area in southeastern Washington, and one radio-instrumented female died overwinter from possible starvation (Knick 1980). In addition, two yearlings collected in eastern Washington were found dead, apparently starved.

Greater use of squirrels by females compared to males in both populations may be the result of females selecting smaller prey than relatively larger males. Fritts and Sealander (1978) showed a greater use of smaller prey items by female bobcats in Arkansas. In contrast, there were no sex-related differences in bobcat diets in eastern Oregon (Toweill 1983). Differential prey exploitation would reduce competition between sexes on shared home ranges (Vaughan 1972).

The greater use of squirrels by kittens compared to adults in western Washington, and mice by kittens compared to yearlings in eastern Washington, suggests that the smaller prey items could be more easily captured by younger animals that had not fully developed hunting skills. Use of mice by kittens, while greater, was not significantly different than by adults in eastern Washington.

The differences in diet between kittens and adults in eastern Washington indicates that young were hunting independently of their mother in this population during this period (Oct.–May). In contrast to our eastern Washington findings, Fritts and Sealander (1978) observed no differences between diets of kittens and adults from stomach samples taken during a period of kitten dependency (Aug.–Nov.)

Table 3. Average weight of bobcat stomach contents by age and sex categories.

	Western Washington		Eastern Washington	
	Average weight	N	Average weight	N
Females	175.6 ± 185.9[a]	111	151.5 ± 185.1	49
Males	263.2 ± 284.8	140	190.1 ± 211.3	34
Adults	252.5 ± 266.4	111	209.9 ± 224.6	31
Yearlings	225.3 ± 293.1	82	135.5 ± 185.5	13
Kittens	169.7 ± 169.5	58	144.1 ± 176.5	39
Total	224.5 ± 223.5	251	167.3 ± 171.5	83

[a] $\bar{x}$ ± SD

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Literature Cited

Crowe, D. M. 1972. The presence of annuli in bobcat tooth cementum layers. J. Wildl. Manage. 36:1330–1332.

———. 1975. Aspects of ageing, growth, and reproduction of bobcats from Wyoming. J. Mammal. 56:177–198.

Erickson, A. W. 1955. An ecological study of the bobcat in Michigan. Unpublished thesis. Michigan State Univ., East Lansing. 133 pp.

Ewer, R. F. 1968. Ethology of mammals. Plenum Publ. Corp. New York. 418 pp.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rept. PNW-8. 417 pp.

Fritts, S. H., and J. A. Sealander, Jr. 1978. Diets of bobcats in Arkansas with special reference to age and sex differences. J. Wildl. Manage. 42:533–539.

Gashwiler, J. S., W. L. Robinette, and O. W. Morris. 1960. Foods of bobcats in Utah and eastern Nevada. J. Wildl. Manage. 24:226–229.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Vol. II. Ronald Press. New York. 1083 pp.

Knick, S. T. 1980. Factors influencing low density bobcat (*Lynx rufus*) populations in southeastern Washington. Unpublished thesis. Washington State Univ., Pullman. 23 pp.

Korschgen, L. J. 1971. Procedures for the food habits analyses. Pages 233–250 *in* R. H. Giles, ed., Wildlife management techniques. Wildl. Soc., Washington, D.C. 633 pp.

Marston, M. A. 1942. Winter relations of bobcats to white-tailed deer in Maine. J. Wildl. Manage. 6:328–337.

McCord, C. M. 1974. Selection of winter habitat by bobcats (*Lynx rufus*) on the Quabbin Reservation, Massachusetts. J. Mammal. 55:428–437.

Moore, T. D., L. E. Spence, C. E. Dugnolle, and W. G. Hepworth. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Dept. Bull. 14. 117 pp.

Morrison, D. F. 1976. Multivariate statistical methods. McGraw Hill Co. New York. 415 pp.

Nussbaum, R. A., and C. Maser. 1975. Food habits of the bobcat (*Lynx rufus*) in the Coast and Cascade ranges of western Oregon in relation to present management policies. Northwest Sci. 49:261–266.

PETRABORG, W. H., AND V. E. GUNVALSON. 1962. Observations on bobcat mortality and bobcat predation on deer. J. Mammal. 43:430–431.

POLLACK, E. M. 1951. Food habits of the bobcat in the New England states. J. Wildl. Manage. 15:209–213.

PROGULSKE, D. R. 1955. Game animals utilized as food by the bobcat in the southern Appalachians. J. Wildl. Manage. 19:249–253.

SCHWARTZ, J. E., II, AND G. E. MITCHELL. 1945. The Roosevelt elk on the Olympic Peninsula, Washington. J. Wildl. Manage. 9:295–319.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

STEELE, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics. McGraw Hill Co. New York. 633 pp.

TOWEILL, D. E. 1983. Winter foods of eastern Oregon bobcats. Northwest Sci. 56:310–315.

VAUGHAN, T. A. 1972. Mammalogy. W. B. Saunders, Philadelphia. 463 pp.

YOUNG, S. P. 1958. The bobcat of North America. Stackpole Co., Harrisburg. 193 pp.

WARM WATER AQUACULTURE USING WASTE HEAT AND WATER FROM ZERO DISCHARGE POWER PLANTS IN THE GREAT BASIN

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Abstract.— Two series of experiments were completed to determine (a) toxicity of waste water from power plants on warm water fish and (b) multiple use of waste heat and water for aquatic animal and plant production. All three types of waste water from a typical coal-fired power plant are acceptable for growing catfish and tilapia following aeration. This growth was compared with fish raised in spring water. Closed, recirculating polyculture systems using evaporation pond water operated efficiently for plant (duckweed) and animal (fish and freshwater prawns) production. Duckweed is an excellent supplement for fish feed. Tilapia and freshwater prawns grew rapidly in the tanks containing duckweed only.

Efficient use of natural resources will be essential in the next decade, especially as it relates to energy reserves. The lower sulfur coal reserves of the western United States are large and are expected to be used as an energy source for many years to come. Design of coal-fired power plants has improved so that more electricity can be produced with minimal impact on the environment. However, plant operation still depends on the availability of large quantities of high-quality water. Although plant efficiency has improved, massive amounts of waste heat is produced and expelled via water-cooling systems. The wasted heat is generally of little use to industry but could be used for warm water aquaculture (Table 1).

Aquaculture involves the farming of economically important species of fish and shellfish (Holden 1978). Aquatic animals tend to have better feed conversion ratios than terrestrial animals, because aquatic animals expend only minimal amounts of energy supporting body weight and in maintaining a constant body temperature.

Development of aquaculture facilities utilizing the tremendous amounts of waste heat produced by power plants should be a goal for maximum use of the coal reserves for the western states. One objective of our research for the past four years has been the development of multiple-use aquaculture systems for the waste heat from power plants in Utah.

Observations of the evaporation ponds at both the Hunter and Huntington power plants in Utah have indicated that at certain times the ponds contain abundant plants and animals and at other times aquatic life is absent. It appears from these observations that a toxin or low dissolved oxygen levels could be responsible for the periodic mortality. These observations led to the initial experimentation to determine probable reasons for this mortality.

It was found in a pilot study that evaporation pond water from the Huntington power plant on occasions was lethal to fish. This

Table 1. Potential uses of thermal waters (adapted from Rinehart 1980).

Degrees (C)	Use
20	Hatching of fish, fish farming
30	Swimming pools, biodegradation, fermentations, de-icing
40	Soil warming
50	Mushroom growing
60	Animal husbandry, greenhouses by combined space and hotbed heating
70	Refrigeration (lower temperature limit)
80	Space heating, greenhouses
90	Drying of stock fish, intense de-icing operations
100	Drying of organic materials, seaweed, grass, vegetables
110	Drying and curing of light aggregate cement slabs
120	Freshwater by distillation, most multiple-effect evaporators, concentration of saline solutions

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TABLE 2. Growth data for long-term toxicity tests. There were 15 catfish and 15 tilapia used in each tank.

Water and animal	Filter system	Initial °WG (gm)	(Ave) L (cm)	40-day WG (gm)	(Ave) L (cm)	60-day WG (gm)	(Ave) L (cm)
COOLING TOWER WATER							
Tilapia	Oyster shell	4.6	4.9	9.9	6.4	19.1	7.98
Catfish	Oyster shell	0.4	2.9	1.3	4.4	3.0	5.9
Tilapia	Bio-ring	5.0	4.5	13.8	7.5	22.6	8.73
EVAPORATION POND WATER							
Tilapia	Oyster shell	4.9	4.7	9.8	6.4	16.6	7.73
Catfish	Oyster shell	0.5	3.0	1.5	4.5	3.3	6.1
Tilapia	Bio-ring	5.5	5.2	12.5	7.0	19.9	8.1
WASTE WATER							
Tilapia	Oyster shell	4.9	4.1	6.4	5.9	12.3	7.1
Catfish	Oyster shell	0.4	3.0	1.8	4.5	3.1	6.2
Tilapia	Bio-ring	4.6	4.6	10.1	6.7	16.5	7.8
SPRING WATER							
Tilapia	Oyster shell	4.6	4.9	8.0	6.2	15.4	7.6
Catfish	Oyster shell	0.4	2.9	1.7	4.9	4.7	6.9
Tilapia	Bio-ring	4.9	4.6	19.3	8.2	28.6	9.4

WG = weight gain, (gm) = grams, L = standard length, (cm) = centimeters

same water could be detoxified using extended aeration. After several hours of aeration, fish were able to live in the water without apparent difficulty. These results prompted further experimentation on the effects of aeration on the toxicity of water used at the Huntington power plant. After this pilot study, two projects were designed and completed to determine multiple use of heated effluent from the power plants.

For project 1, experiments were designed to duplicate previous toxicity testing and to determine long-term fish survival in waste water. The project included short-term (8 day) toxicity using catfish (*Ictalurus punctatus*) and long-term (60 day) toxicity using biological filtration, in which two types of media and two species of fish, catfish and *Tilapia aurea*, were included. The filter media included a high calcium filter medium (bro-

TABLE 3. Growth and survival for long-term toxicity tests. There were 15 catfish and 15 tilapia used in each tank.

Water and animal	Filter system	60-day °WG (gm)	Increase (%)	60-day Mortality (%)
COOLING TOWER WATER				
Tilapia	Oyster shell	314	63	13
Catfish	Oyster shell	650	103	0
Tilapia	Bio-ring	353	94	27
EVAPORATION POND WATER				
Tilapia	Oyster shell	240	64	20
Catfish	Oyster shell	546	103	7
Tilapia	Bio-ring	262	55	27
WASTE WATER				
Tilapia	Oyster shell	150	72	13
Catfish	Oyster shell	688	105	0
Tilapia	Bio-ring	260	70	13
SPRING WATER				
Tilapia	Oyster shell	235	54	0
Catfish	Oyster shell	1050	137	60
Tilapia	Bio-ring	483	104	53

°WG = weight gain, (gm) = grams

TABLE 4. Large-system lower tank (weights, feed, conversions). There were 20 catfish and 20 tilapia used in this tank. Day 1 = 25 Feb 1981.

	Fish weights (g)			Feed (g/Period)		Conversion/Period (Feed/Flesh)
Day	Catfish	Tilapia	Total	Duckweed	Commercial	
1	58.4	182.6	241.0			
14	104.3	265.8	370.1		78.0	0.60:1
30	145.0	400.8	545.8		148.8	0.85:1
45	213.2	619.2	832.4		257.1	0.90:1
60	186.7	590.4	771.1	691.5	—	—
75	178.8	608.5	787.3	1631.0°	—	15.99:1
91	124.0	695.5	819.5	1576.0°	105.4	8.17:1
100	155.9	761.5	917.4	1106.1°	73.8	1.88:1
117	230.5	930.0	1160.5	2201.6°	147.2	1.51:1
132	293.5	1202.0	1495.5	54.0°	273.2	0.83:1

Total gain = 1254.5 g
Total feed – Duckweed = 726.0 g dry wt
Total commercial feed = 1083.5 g
Overall conversion = 1.44:1 (0.58 duckweed/g + 0.86 comm.[)
°Duckweed from an outside source

ken oystershell) and commercial plastic biorings. For the second project a polyculture system, using the same two types of warm water fish, two species of aquatic plants, and a freshwater prawn, was outlined using closed water systems. These organisms were chosen because of their compatibility, high productivity, and marketability (Suffern 1980, Dunseth 1977). An added advantage is that aquatic plants remove nitrogen from the system, helping to maintain good water quality while providing a useful product (Hillman and Culley 1978, Williams 1976).

METHODS AND MATERIALS

Project 1

Fish toxicity trials for Project 1 were conducted using water from the evaporation pond, cooling towers, and neutralizing basin at the Huntington Power Plant and from a freshwater spring located at Brigham Young University. Water from each source was placed in three one-gallon jars. One jar from each water type was included in one of three groups consisting of four jars each. Water in jars of the first group was aerated for 72 hours prior to the addition of fish. Water in the second group was aerated for 24 hours prior to receiving fish. Water in the third group was not aerated and fish were added immediately after the jar was filled. Five fingerling catfish were placed in each jar at the beginning of the study. All jars were then aerated continuously for the eight-day duration of the experiment.

Long-term toxicity testing was conducted using 10-gallon aquaria. Two aquaria were

TABLE 5. Large-system upper tank (weights, feed, conversions). There were 20 catfish and 20 tilapia used in this tank. Day 1 = 25 Feb 1981.

	Fish weights (g)			Feed (g/Period)	Conversion/Period (Feed/Flesh)
Day	Catfish	Tilapia	Total		
1	48.3	193.9	242.2		
14	75.2	272.6	347.8	79.3	.75:1
30	119.4	377.5	496.9	139.2	.93:1
45	157.8	541.9	699.7	223.2	1.10:1
60	200.7	725.0	925.7	262.5	1.16:1
75	261.0	937.0	1198.0	324.8	1.19:1
91	280.8	976.7	1257.5	420.0	7.06:1
100	319.2	1063.4	1382.6	282.6	2.26:1
117	347.2	1127.5	1474.7	553.6	6.01:1
132	411.0	1308.0	1739.0	479.7	1.81:1

Total gain = 1496.8 g
Total commercial feed = 2764.9 g
Overall conversion – 1.85:1

Table 6. Small-system lower tank (weights, feed, conversions). There were 10 catfish and 10 tilapia used in this tank. Day 1 = 25 Feb 1981.

Day	Fish weights (g)			Feed (g/Period)	Conversion/Period (Feed/Flesh)
	Catfish	Tilapia	Total		
1	28.2	123.4	151.6		
14	42.6	183.8	226.4	79.3	0.66:1
30	45.0	251.7	296.7	91.2	1.30:1
45	62.7	354.1	416.8	133.2	1.11:1
60	93.5	446.8	540.3	156.0	1.26:1
75	10.5	237.0	247.5	165.5	—*
91	16.5	333.7	350.2	93.0	7.06:1
100	20.0	348.1	368.1	79.2	2.26:1
117	39.0	459.0	498.0	147.2	6.01:1
132	42.0	564.0	606.0	162.5	1.81:1

Total gain = 454.4 g
Total commercial feed = 1077.2 g
Overall conversion - 2.37:1 (due to high mortality from day 60–75)
*Mortality due to low D.O. and feeding stress

plumbed together to form one system. Each system consisted of one aquarium acting as a filter while the second acted as a habitat for fish. Twelve systems were divided into three groups consisting of four systems each.

Oystershell was used as a filter medium in two of the three groups, and the remaining group contained plastic bio-rings. Fifteen fingerling catfish were placed in one of the oyster shell groups. Fifteen tilapia were placed in each of the systems in the second oyster shell group. The group using bio-rings received fifteen fingerling tilapia. All fish were weighed and measured (standard length) prior to the beginning of the experiment. The 15 catfish in each tank were weighed as a group because of their small size.

Four water types were used for experimentation within each group. These consisted of water from the cooling tower, evaporation pond, waste water basin of the Huntington Power Plant, and the BYU spring. Water quality parameters of temperature, pH, nitrite, and conductivity were taken weekly.

Project 2

Two closed, recirculating systems were constructed, each involving a sequence of five tanks. Two tanks in each system contained equal numbers of tilapia and channel catfish. The fish in these two tanks were fed a commercial trout diet at the rate of 2.5% of the fish's body weight adjusted at 15-day intervals according to the growth of the fish. For the other tanks, two per system had duckweed (*Lemna minor*) floating on the water surface. One of the duckweed tanks in

Table 7. Small-system upper tank (weights, feed, conversions). There were 10 catfish and 10 tilapia used in this tank. Day 1 = 25 Feb 1981.

Day	Fish weights (g)			Feed (g/Period)	Conversion/Period (Feed/Flesh)
	Catfish	Tilapia	Total		
1	28.5	96.0	124.5		
14	30.0	140.5	170.5	40.3	0.88:1
30	43.1	180.0	223.1	60.8	1.16:1
45	61.0	275.5	336.5	100.8	0.89:1
60	94.0	378.5	472.5	126.0	0.93:1
75	118.0	474.5	592.5	165.2	1.38:1
91	94.3	506.2	600.5	217.0	27.13:1*
100	119.7	536.5	656.2	135.0	2.42:1
117	170.5	603.0	773.5	262.4	2.24:1
132	203.0	717.0	920.0	250.9	1.71:1

Total gain = 795.5 g
Total feed = 1358.4 g
Overall conversion - 1.71:1
*High conversion due to mortality from day 75–91

each system received freshwater shrimp (*Macrobrachium rosenbergii*) and the other received 2 tilapia each. No commercial food was added to the duckweed tanks, leaving the shrimp and tilapia in these tanks to feed on plant growth and waste products coming from the other fish tanks. The fifth tank contained the biological filter that consisted of a crushed oyster shell and the nitrifying bacteria. One filter tank also contained pots of water chestnuts (*Eleocharis dulcis*).

The water flowed through a duckweed tank, a fish tank, the second duckweed tank, the second fish tank, then into the filter. Water from the filter tank was recirculated back into the first duckweed tank. Water quality parameters were measured daily and fish growth was measured every 15 days. Duckweed was harvested as necessary to prevent clogging of pipes and filters and to promote maximum duckweed growth.

In addition to the laboratory system, a cage (4 × 4 × 4 ft, floating, of rubber-coated mesh) was placed in the evaporation pond at the Hunter Power Plant. Fifteen tilapia were placed in the cage and their growth was monitored.

TABLE 8. Duckweed production (Starting 25 Feb 1981) in the large-system upper tank.

Date	Amount harvested (g)
2 April	458.2
20	698.9
12 May	275.0
20	126.0
27	327.0
4 June	286.0
8	129.0
15	135.0
16	135.0
17	135.0
19	135.0
20	135.0
23	44.0
25	102.0
26	45.0
27	57.0
29	45.0
30	110.0
1 July	63.0
2	40.0
6	65.0
Total*	3546.1

*Total = 3546.1 g = 36.7 tons/acre/year.

RESULTS

Project 1

All but two fish used in the short-term toxicity tests survived the eight-day duration of the experiment. The two deaths occurred in evaporation pond water, one in the 72-hour jar and one in the 24-hour jar.

Mortality in the long-term experiments resulted in 10 dead catfish and 6 dead tilapia in the oyster-shell-filtered groups. Eighteen tilapia died in the bio-ring-filtered group. The 10 catfish included one in evaporation pond water and 9 in spring water. The tilapia mortality in the oyster shell group included 2 each in evaporation pond water, waste water, basin water, and cooling tower water. Mortality in the bio-ring system included 4 each in evaporation pond water and cooling tower water, 8 in spring water, and 2 in the water from the waste water basin.

Water quality was acceptable in the oyster shell system during the experimental period; however, nitrite levels in the bio-ring group were well below acceptable levels. Growth data is reported in Tables 2 and 3.

Project 2

Tilapia fed the prepared trout food showed increases in body weight of 10 to 50% every 15 days (Tables 4–7). When fed strictly duckweed at 15% of body weight, the tilapia showed marginal gains but the catfish lost weight (Table 4 between days 45–75). When a mixture of duckweed and trout food was fed, weight gains of up to 28% were achieved (Table 4). The conversion ratios were best

TABLE 9. Duckweed production (Starting 25 Feb 1981) in the small-system upper tank.

Date	Amount harvested (g)
2 April	317.1
22	266.0
12 May	319.5
23	170.0
30	192.0
2 June	142.0
13	140.0
21	70.0
Total*	1616.6

*Total = 1616.6 g = 38.9 tons/acre/year.

when duckweed and commercial feed were used together (Table 4). The tilapia and shrimp in the duckweed tanks grew rapidly without being fed any outside food, eating only the existing plant growth and waste products. Duckweed production has been measured at approximately 33 tons/ac/yr (Tables 8–10). Duckweed in the large-system lower tank did not have a chance to reproduce before the fish in the tank ate it. The small system that had contained the power plant evaporation pond water since day 77 (Tables 11 and 12) experienced a spawning on day 117 in the lower fish tank. The newly hatched fish were removed from the fish tank and placed in the duckweed tanks. As of August they were nearly 1.5 inches long, feeding entirely on duckweed and waste products in the system. Some mortality of fish was experienced due to low dissolved oxygen (D.O.) at times. The low dissolved oxygen was probably due to the high respiration from plant materials growing in the system and the biologic filter organisms. To compensate for the problem, air stones were added.

The water chestnuts grew poorly under the normal fluorescent lights but did well under the broad spectrum lights. At the Hegerhorst system in Benjamin, Utah, water chestnuts from the same stock, planted outside at the same time, grew to approximately 5 feet tall and have been harvested.

It can be seen that the large system reacted the same as the small system, but not as quickly. The biological filters required a normal period of time to establish themselves, as shown by the nitrite levels, but were sufficient to handle 2.5% feed rates.

TABLE 10. Duckweed production (Starting 25 Feb 1981) in the small-system lower tank. Two fish were included in this tank.

Date	Amount harvested (g)
2 April	250.8
22	139.7
21 May	203.0
8 June	121.0
14	138.0
21	70.0
24	54.0
Total*	975.7

*Total = 975.7 g = 23.4 tons/acre/year.

The evaporation pond at Hunter during July and August 1981 contained mayflies, dragonflies, damselflies, numerous water beetles, and abundant vegetation. The fish in the cage were given no food except for some of the mosses and aquatic insects that existed in the pond. The fish grew very well on the natural productivity of the pond, increasing 64% in weight in one month (Table 13).

DISCUSSION

Results from short-term and long-term tests indicate that all the waters used in this experiment were acceptable for growing both species of fish under the defined conditions. Animal growth was considered to be satisfactory in all systems. The high mortality rate in the spring water aquaria was probably due to contamination of the water line, because the spring water pumps were being repaired the day prior to beginning the experiments.

The results of the short-term toxicity testing were surprising because there was much less mortality than was expected. It appeared that none of the water sources contained the substances that had produced toxicity in the past. One possible explanation for this lack of toxicity might be that the toxin or toxins are not continuously present in the waste waters from the power plant. Therefore, the toxin may be the result of some variation in the normal processes of the power plant.

Discussion with personnel at the power plant indicated that periodically the blowdown from the SO_2 scrubbers have been released into the evaporation pond. It was also found that changes have been made to prevent this from occurring in the future. It appeared likely that this blowdown may have been the source of the periodic toxicity observed in the evaporation pond. Examination of fish tissue using EDAX (Energy Dispersive

TABLE 11. Water quality for large system.

Parameter	Mean	Range
Temperature (centigrade)	26.8	23.0–31.0
pH	7.7	7.4–8.5
Conductivity	535	250–800
Oxygen (ppm)	3.95	1.62–7.2

Analysis for X-Rays) in conjunction with SEM (Scanning Electron Microscopy) indicated high levels of sulfur that further confirmed this hypothesis. The EDAX technique can detect elements found in tissue in ppm and ppb.

The advantages and potential of this type of aquaculture system are great. The present data indicate that the closed, recirculating polyculture system will operate efficiently, especially when duckweed from within the system is used as a supplemental feed. This corroborates other findings (Mayo 1976, Ray 1981, Siddal 1974). It is reported that 75–80 percent of the production costs in aquaculture come from the feed and fingerlings (USDA Economic and Statistical Service 1981). Duckweed as a supplement could be an important factor in cutting back these costs. The economic values of a polyculture system are obvious because there is more production per unit of culture. Our tests have also shown that there is no apparent effect upon the organisms using waste waters from Utah Power and Light's Hunter Unit, and, thus, on the basis of our tests, it appears that the water can be used directly in the aquaculture system. Although this system will produce a protein source suitable for human consumption, it will also produce other benefits that have been summarized below:

1. The system will provide a secondary method for the consumption of waste heat, drawing required amounts of heat directly from water lines carrying waste heat to the cooling towers.
2. This system could allow additional use of heat and water from geothermal projects prior to water reinjection.
3. Water flowing from aquaculture operations will carry nutrients beneficial to surface farming operations.
4. The aquaculture operations are nonconsumptive. Water losses will be limited to evaporation.
5. Duckweed production from aquaculture ponds can be used as a protein supplement for cattle. Up to 75% replacement of cattle feed by duckweed has been tested successfully by other researchers (Hillman and Culley 1978).

TABLE 12. Water quality for small system.

Parameter	Mean	Range
Temperature (centigrade)	27.2	25.0–30.0
pH	7.7	7.2–8.4
Conductivity	510/4930°	440–600/2900–7000
Oxygen (ppm)	5.14	1.26–7.80

°Higher conductivity levels are the result of the change from spring water to evaporation pond water.

LITERATURE CITED

DUNSETH, D. R. 1977. Polyculture of channel catfish (*Ictalurus punctatus*), silver carp (*Hypophthalmichthys molitrix*), and three all male tilapias (*Sarotherodon* spp.). Unpublished dissertation. Auburn Univ. 62 pp.

HILLMAN, W. S., AND D. D. CULLEY, JR. 1978. The uses of duckweed. Amer. Scientist 66:442–451.

HOLDEN, C. 1978. Government seeking ways to encourage aquaculture. Science 200:33–35.

MAYO, R. D. 1976. A technical and economic review of the use of reconditioned water in aquaculture. Aquaculture 1976:508–520.

RAY, L. 1981. Channel catfish and tilapia production in geothermal water. Paper given at the Annual Meetings of the Soil Conservation Society of America, 2–5 August, Spokane, Washington.

RINEHART, J. S. 1980. Geysers and geothermal energy. Springer Verlag, Berlin.

SIDDAL, J. 1974. Studies of closed marine culture systems. Prog. Fish Cult. 36(1):8–15.

TABLE 13. Cage culture at the Hunter Power Plant in 1981.

20 July		15 August	
Length (mm)	Weight (g)	Length (mm)	Weight (g)
175	91	128	37
128	37	147	52
170	82	176	102
134	38	183	117
175	100	184	112
156	65	125	43
114	24	140	58
123	31	151	76
144	48	147	69
125	31	133	46
120	24	150	75
130	31	152	73
132	38	154	76
113	19	152	84
135	39		

20 July 1981
Mean length = 138.3 mm Mean Wt. = 46.5 g
Range = 113 – 175 mm Range = 19 – 100 g
Std Dev = 21.2 Std Dev = 25.7

15 August 1981
Mean length = 151.6 mm Mean Wt. = 72.9 g
Range = 125 – 184 mm Range = 37 –c117 g
Std Dev = 18.5 Std Dev = 24.9
Increase = 38% Increase = 64%

Suffern, J. S. 1980. The potential of tilapia in U.S. aquaculture. Aquaculture 6:14–18.

U.S. Department of Agriculture, Economics and Statistics Service. 1981. Aquaculture outlook and situation report. U.S. Government Printing Office, Washington, D.C.

Williams, A. K. 1976. Chinese water chestnut culture. *In* Horticultural crops. Richard B. Russell Agricultural Research Center, Athens, Georgia.

CENTRIC DIATOMS OF LAKE TAHOE

Albert D. Mahood[1,2], Robert D. Thomson[1,3], and Charles R. Goldman[1]

Abstract.— An understanding of the mechanisms of phytoplankton species interaction is dependent on a precise knowledge of what species exist within the community. The centric diatoms of Lake Tahoe, California-Nevada, which are often the dominant component of the phytoplankton community, are presented in both light and scanning electron microscopy (SEM) photographs. Specific attention has been given to initial cell forms of *Cyclotella stelligera* Cleve and Grunow and *C. comta* (Ehrenberg) Kützing through the aid of the SEM.

Lake Tahoe, formed by a graben fault, is a remarkably unproductive subalpine environment. Currently under the influence of rapid urbanization as a year-round resort area, it is beginning to show signs of the earliest stages of eutrophication (Goldman 1974).

As was the case with most of the biological sciences, the early interest in taxonomy characterized the beginning stages of limnology. With the development of new techniques for measuring biological processes (such as photosynthesis and respiration) in lakes, emphasis on taxonomy declined and studies of community metabolism became a major thrust in limnological research. The study of the limnology of Lake Tahoe during the past 20 years has stressed primary productivity, response to nutrients by algae, and water chemistry of the lake and its tributaries. With further advances in the study of lake processes, it became apparent that an understanding of the mechanisms of phytoplankton species interaction with one another and with their chemical-physical environment is prerequisite to the understanding of dynamic processes in the lake. Thus, aquatic biologists have returned by necessity to research at the species level that requires a renewed interest in taxonomic work. Periodically the phytoplankton community of Lake Tahoe is dominated by diatoms. The large number of diatoms and their role as water quality indicators have stimulated an increasing emphasis on taxonomic studies of diatoms in an ongoing limnological research program at Lake Tahoe, conducted by the Tahoe Research Group of the University of California, Davis. Although diatoms continue to be the most common dominants of Lake Tahoe, recent research shows that a few species other than diatoms (particularly small, spheroid green or yellow-green algae) have become significant contributors to the phytoplankton community (Tilzer and Goldman 1978). This may have resulted, in part, from a drastic change in the grazing zooplankton population caused by the introduction of the opossum shrimp, *Mysis relicta* (Goldman et al. 1979).

This paper is presented to establish an accurate, practical reference to the centric diatoms of Lake Tahoe. Species identification was established and verified in this study through collaborative identification of specimens by authorities in diatom taxonomy. To assist future investigators, the original individually mounted slides of verified species are deposited at the Department of Geology, California Academy of Sciences, San Francisco, and an additional set of slides and reference material is stored at the Division of Environmental Studies, University of California, Davis.

Materials and Methods

Phytoplankton samples were collected in van Dorn samplers as described by Goldman (1974). Periphyton samples were collected

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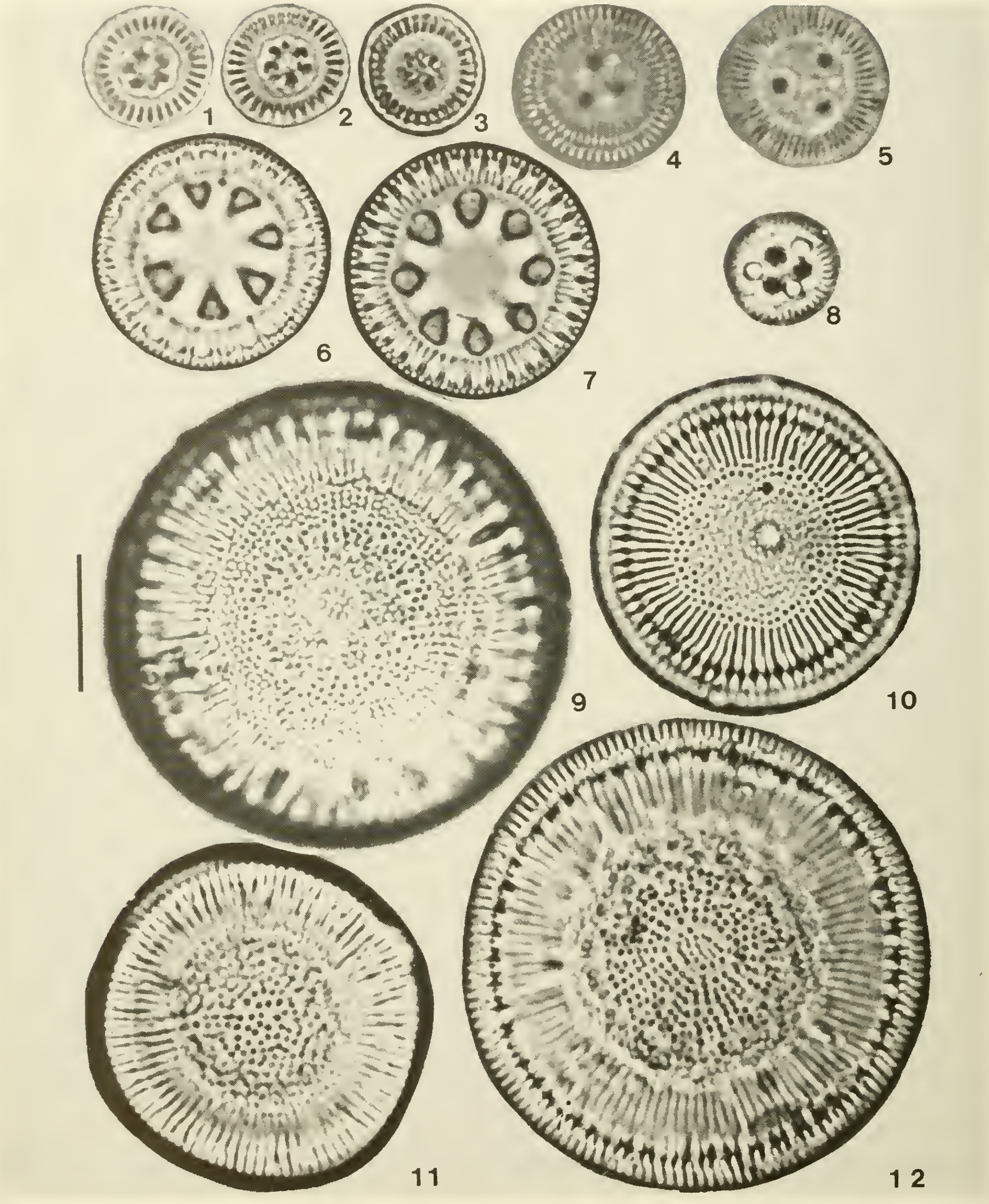
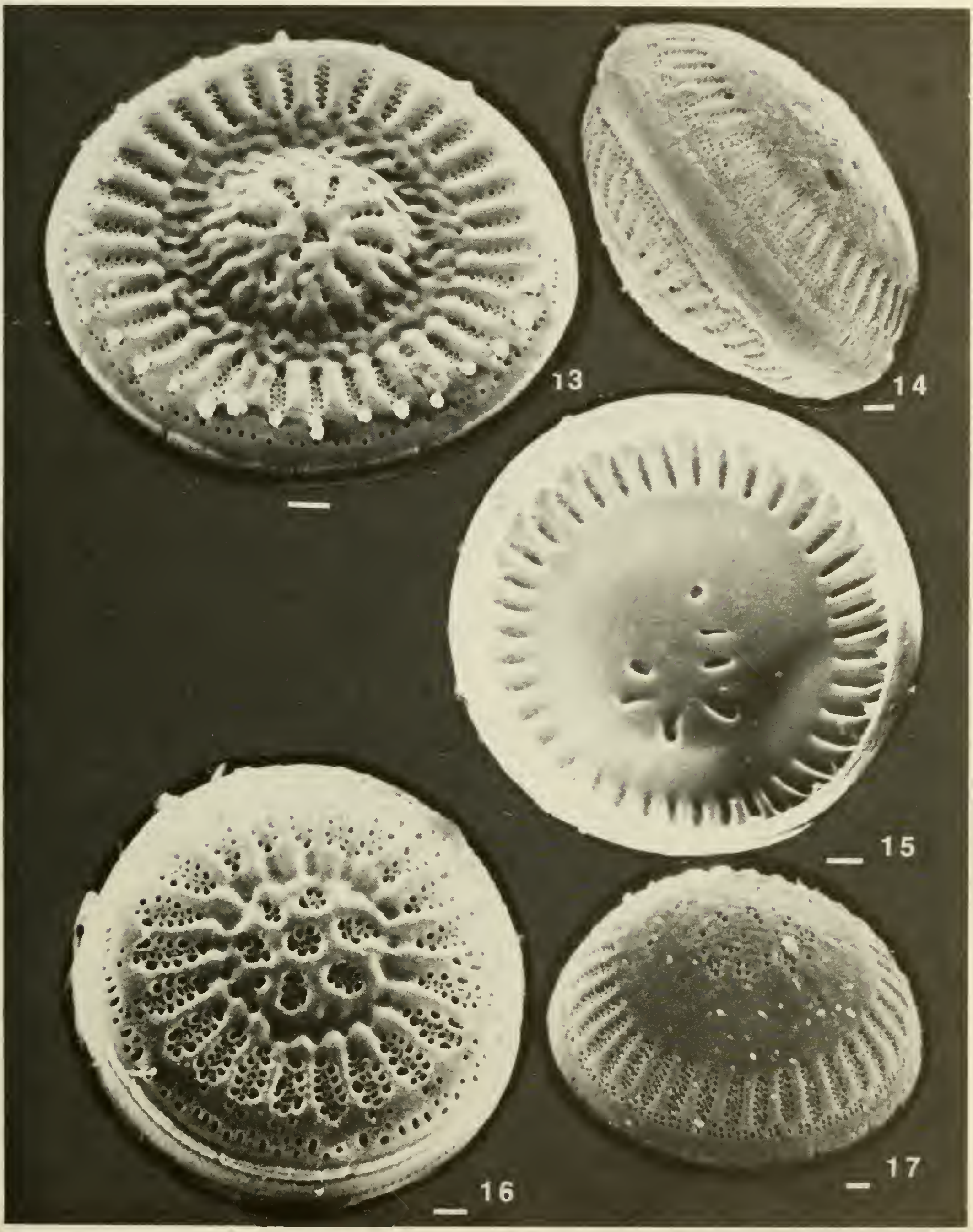


Figs. 1–12. *Cyclotella* spp.: 1, *C. stelligera*, valve view, stellate central area; 2, *C. stelligera*, valve view, marginal striae; 3, *C. stelligera*, internal valve view; 4, *C. ocellata*, external valve view; 5, *C. ocellata*, internal valve view; 6, *C. antiqua*, valve view, conical structures in central area; 7, *C. antiqua*, pronounced marginal striae; 8, *C. ocellata*, whole cell, 9, *C. comta*, areolate pattern at junction of striae and central area; 10, *C. comta*, isolated puncta, labiate pore, at the end of shortened striae; 11, *C. comta*, irregular alveolae pattern in central area; 12, *C. comta*, typical external view of valve. Scale = 10 μm. LM.

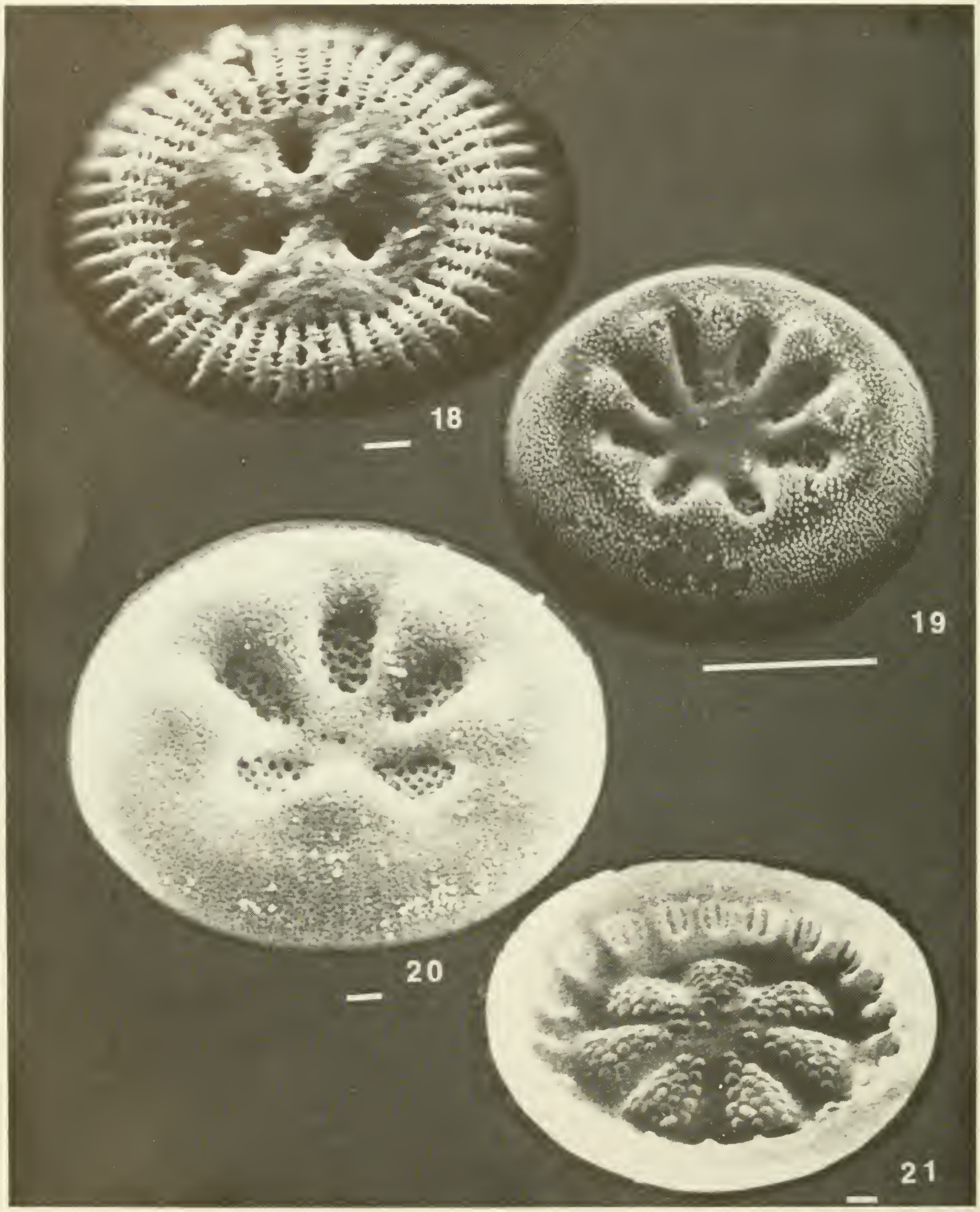
from artificial substrates made of Pyrex glass cylinders (Goldman 1974) or from the natural rock substrates found in the lake.

The cleaning and mounting of fossil as well as recent diatom material has been extensively discussed by Van Heurck (1896), Mea-



Figs. 13–17. *Cyclotella stelligera*: 13, external valve view, stellate central pattern with central areolae structure; 14, girdle view of initial cell; 15, internal view of initial cell, irregular stellate pattern; 16, external view of whole cell; 17, external valve view of initial cell. Scale = 1 μm. SEM.

kin (1939), Hendey (1964), Patrick and Reimer (1966), Lohman (1972), and Mandra et al. (1973). The techniques that were most appropriate for the relatively small species of *Cyclotella* and *Melosira* were variations of those procedures developed by Hanna (1930),



Figs. 18–21. *Cyclotella* spp.: 18, *C. ocellata* (SEM), external view of partially decomposed valve (scale = 1 μm); 19, *C. antiqua*, external valve view (scale = 10 μm); 20, same, external valve view, partially cleaned valve (scale = 1 μm); 21, same, internal view (scale = 1 μm).

Meakin (1939), Lohman (1972), and Van der Werff (1955). The Van der Werff technique, using a succession of treatments with hydrogen peroxide, potassium permanganate, and oxalic acid, proved to be the least destructive.

Light microscope (LM) observations and photographs were taken with an Olympus

IMT, using Kodak High Contrast Copy film. Scanning electron microscopy (SEM) observations and photographs were taken with a Cambridge S-180.

SYSTEMATICS

Classification of the higher taxa of centric diatoms follows the scheme set forth by Patrick and Reimer (1966). Classification of individual species follows the systematics as proposed by Van Landingham (1967, 1969).

Division	Bacillariophyta
Class	Bacillariophyceae
Order	Eupodiscales
Family	Coscinodiscaceae
Genera	*Melosira* Agardh *Cyclotella* Kützing *Stephanodiscus* Ehrenberg

Cyclotella antiqua W. Smith
Figs. 6,7,19–21

References: Hustedt 1930: 102, Fig. 75; Cleve-Euler 1951:43, Fig. 51; Schmidt 1900: Pl. 224, Fig. 45. California Academy of Sciences No. 60944.

The cells are cylindrical, valves slightly concave. The diameter varies from 15–23 μm. Because of the broadly rounded marginal zone (Figs. 19,20), the margin appears narrow, approximately one-third the radius. This species is characterized by the 5–8 conical depressions in the central zone, filled with irregularly arranged areolae. The apex of the cone is directed toward the central area. The valve is covered by fine radiating punctae (Figs. 19,20).

Distinguishing characteristics: 5–8 conical depressions in the central zone.

Distribution in Lake Tahoe: infrequent.

Ecology: oligotrophic (Stoermer and Yang, 1969).

Cyclotella comta (Ehr.) Kützing
Figs. 9–12, 22–30

Reference: Hustedt 1930: 99, Fig. 69. CAS No. 61078.

The cells are cylindrical with concentrically undulating valves. The valves are concave or convex. Species from Lake Tahoe vary from 15–40 μm in diameter. The marginal striae form a zone approximately half the radius. At the margin of the valve, the alveolae (Figs. 24,25) appear as short darkened striae under the light microscope (Fig. 12). The areolae of the central area are radiating or irregular (Figs. 22,23). This species clearly displays 2–3 well-defined labiate processes set out by shortened marginal striae. The labiate processes are not as well developed in the initial cell form as they are in the valve of later developed cells (Figs. 27,30).

Distinguishing characteristics: isolated punctae and shortened dark marginal substructures.

Distribution in Lake Tahoe: common.

Ecology: alkaliphilous, oligohalobus (indifferent), mesosoprobic, euplanktonic (Lowe 1974), eutrophic (Van der Werff 1957).

Cyclotella ocellata Pantocsek
Figs. 4,5,8,18

References: Pantocsek 1902: Pl. 15, Fig. 318; Hustedt 1930: 100, Fig. 68; Schmidt 1906: Pl. 266, Figs. 8,9; Cleve-Euler 1951: Figs. 64s–v. CAS No. 60946.

Cells cylindrical, always found singly. Valve surface flat to slightly concave. Valve diameters from 8–11 μm. The marginal striae are irregular, 15 in 10 μm. The marginal striae zone is slightly less than half the radius in width. The central area is usually found with three distinct, symmetrically distributed areolae, although specimens with 4–5 areolae have been observed. Cleve-Euler (1951) has suggested that *C. ocellata* be included within the species *C. kutzingiana* (Thwaites) Chauvin as the variety *planetophora*. *C. ocellata* has not been found in sufficiently large numbers to give more definitive diameters or structural variations.

Distinguishing characteristics: Large punctae in the central area symmetrically arranged.

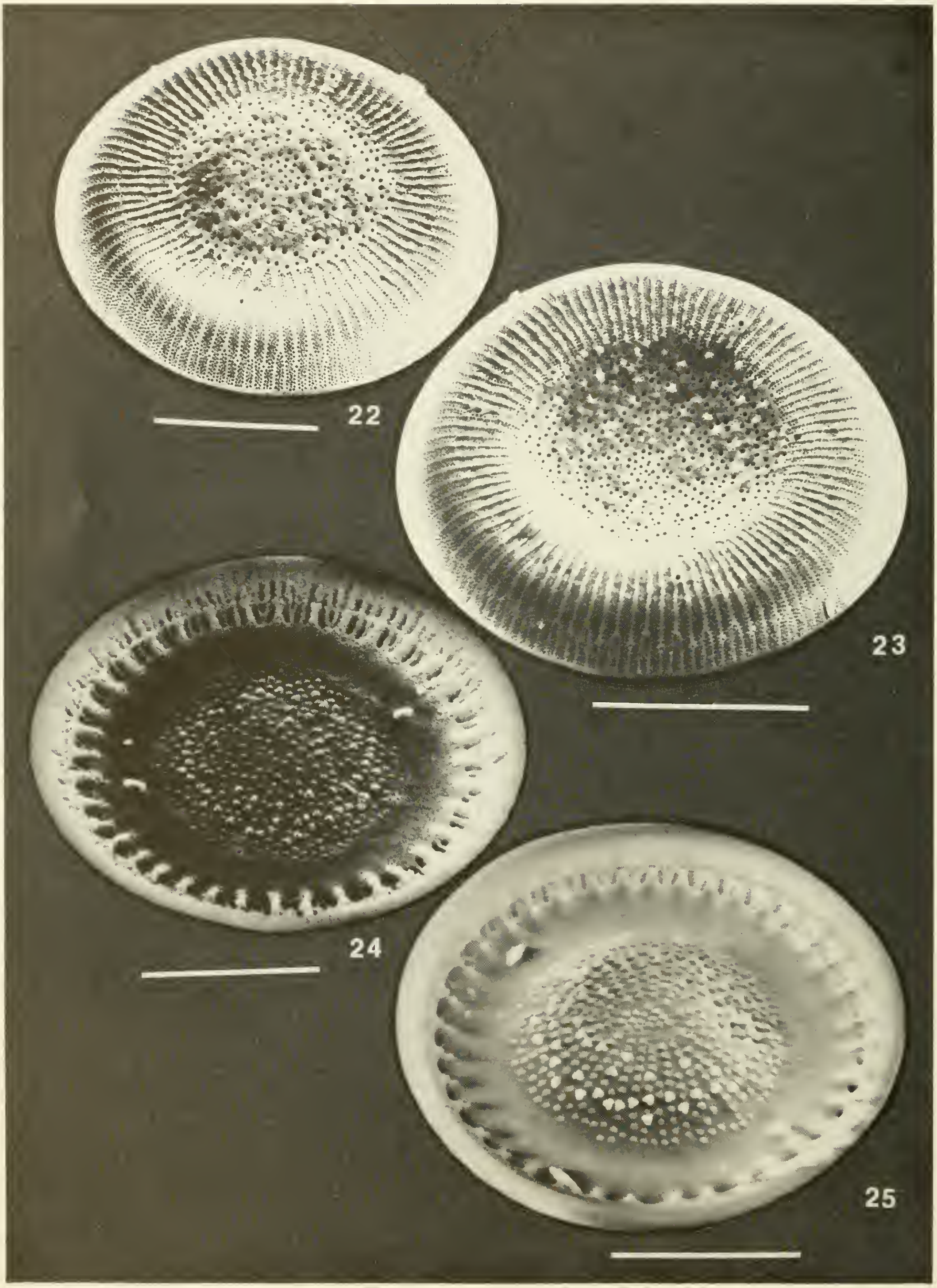
Distribution in Lake Tahoe: infrequent.

Ecology: alkaliphilous, oligohalobus (indifferent), periphytic (Lowe 1974).

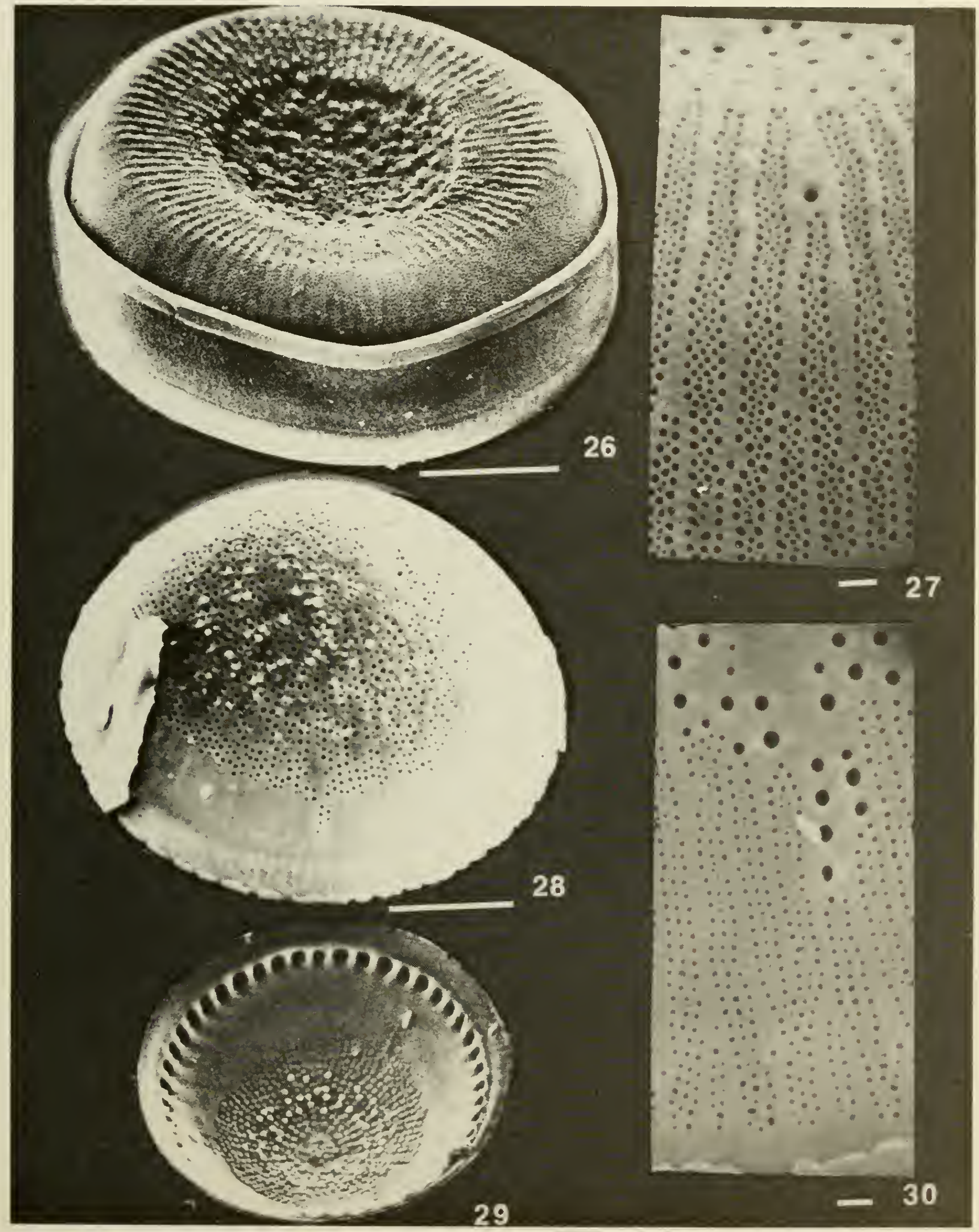
Cyclotella stelligera Cleve and Grunow
Figs. 1–3,13–17

References: Hustedt 1930: 100, Fig. 65; Cleve-Euler 1951: 43, Fig. 52. CAS No. 60947.

The single cylindrical cells are concentrically undulated, with the marginal striae zone one-third the radius. Ornamentation of the marginal zone is composed of

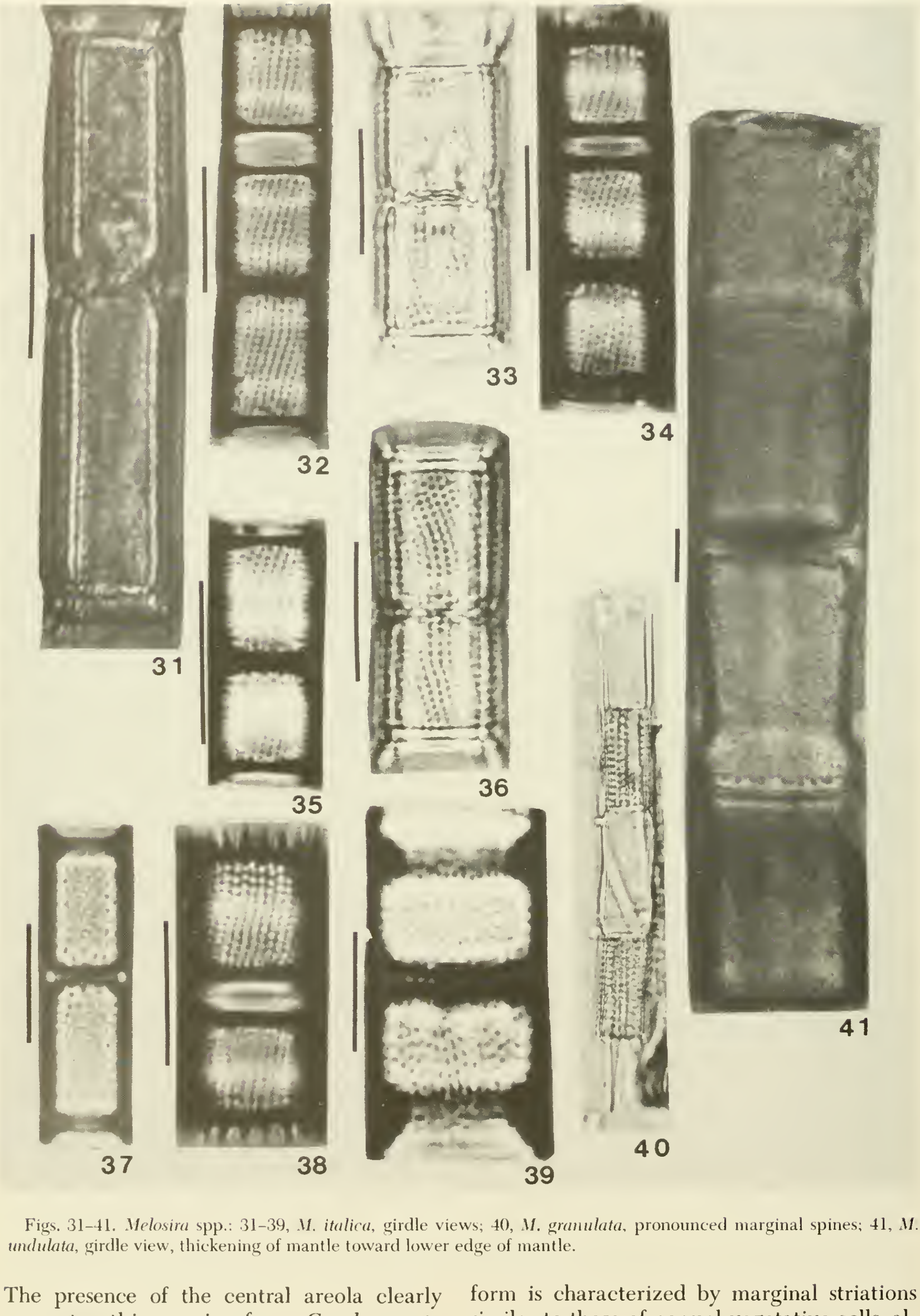


Figs. 22–25. *Cyclotella comta*: 22, external view of convex valve, irregular central area, two isolated labiate pores within the marginal striae; 23, external view concave valve; 24, internal view, concave valve, two labia across from one another; 25, internal view of concave valve, radial alveolae pattern. Scale = 10 μm. SEM.



Figs. 26–30 *Cyclotella comta* (SEM): 26, external view of whole cell (scale = 10 μm); 27, detail of labiate pore of vegetative cell (Fig. 23) (scale = 1 μm); 28, external view of initial cell (scale = 10 μm); 29, internal view of initial cell (scale = 10 μm); 30, detail of labiate area of initial cell (Fig. 28) (scale = 1 μm).

prominent alveolate striae, 10–12 in 10 μm. These striae are composed of small areolae (Figs. 13,16). The central area is composed of a single large areola surrounded by a stellate arrangement of 5–6 areolae, although the stellate arrangement may vary considerably.



Figs. 31–41. *Melosira* spp.: 31–39, *M. italica*, girdle views; 40, *M. granulata*, pronounced marginal spines; 41, *M. undulata*, girdle view, thickening of mantle toward lower edge of mantle.

The presence of the central areola clearly separates this species from *C. glomerata* Bachmann. Ornamentation of the initial cell form is characterized by marginal striations similar to those of normal vegetative cells, although the central area of the initial cell is more irregularly arranged (Fig. 15). The initial cell is spherically developed and can be distinguished from the flat or slightly convex vegetative cells (Figs. 14,17). *C. stelligera* from Lake Tahoe vary from 3–11 μm in diameter.

Distinguishing characteristics: stellate arrangement of the central areolae with a central areola.

Distribution in Lake Tahoe: frequent.

Ecology: eutrophic, oligohalobus (indifferent), periphytic (Lowe 1974).

Melosira distans var. *alpigena* Grunow

Figs. 39,48

The cells are cylindrical, with the valve mantles parallel. The poroid ornamentation of the valve is parallel to the pervalvar axis. The margin of the valve is furnished with relatively short spatulate spines (Fig. 48) that mesh with the adjacent cell.

Distinguishing characteristics: The mantle is shorter than *M. italica* (Ehr.) Kützing and more heavily silicified (Stoermer and Yang 1969).

Distribution in Lake Tahoe: rare.

Ecology: acidophilous, oligotrophic, oligosaprobic (Van der Werff 1957), oeriphytic (Lowe 1974).

Melosira granulata (Ehr.) Ralfs

Fig. 40

Reference: Hustedt 1930: 87, Fig. 44

The cells are cylindrical, valve mantle parallel, valve face flat, with poorly developed pseudosulcus. The ornamentation of the valve is variable. The valve margin is furnished with a corona of irregular spines with longer spines overlapping the next cell in the colony. In a few cells observed, spines often extended the length of the mantle of the next cell. Alveolae are arranged obliquely along the pervalvar axis. So few individuals of the species were found in the samples that no reasonable estimate of the species size could be made. Hustedt (1930) found the range to be 5–21 μm in diameter and 5–18 μm in mantle height.

Distinguishing characteristics: irregular, long marginal spines.

Distribution in Lake Tahoe: rare in plankton, common in Emerald Bay periphyton.

Ecology: alkaliphilous, eutrophic, oligohalobous (indifferent), euplanktonic (Lowe 1974).

Melosira italica (Ehr.) Kützing

Figs. 31–38,46,47

References: Hustedt 1930: 92, Fig. 52; Cleve-Euler 1951: 26, Fig. 16e. CAS No. 60949.

The cells are cylindrical, valve mantle parallel, valve face flat, with an extremely small pseudosulcus. Under the light microscope the pseudosulcus appears deeply incised, forming a right angle with the mantle. The sulcus extends about half the radius of the lumen (Fig. 47). The valve surface is irregularly alveolate. The margin of the valve is furnished with a corona of small spines that mesh with the corresponding structures of the adjacent cell (Fig. 46). Ornamentation of the valve mantle is composed of a linear to spiral arrangement of circular to elongate alveolae (Figs. 36,38,46). The valve mantle varies, 6–17.5 μm in length, and the valve diameter varies from 6.5–18 μm.

Distinguishing characteristics: corona with regular denticulate structures and lacking the pronounced spine of *M. granulata*. *M. italica* can be distinguished from *M. ambigua* (Grun.) O. Müller by the extremely small pseudosulcus.

Distribution in Lake Tahoe: common.

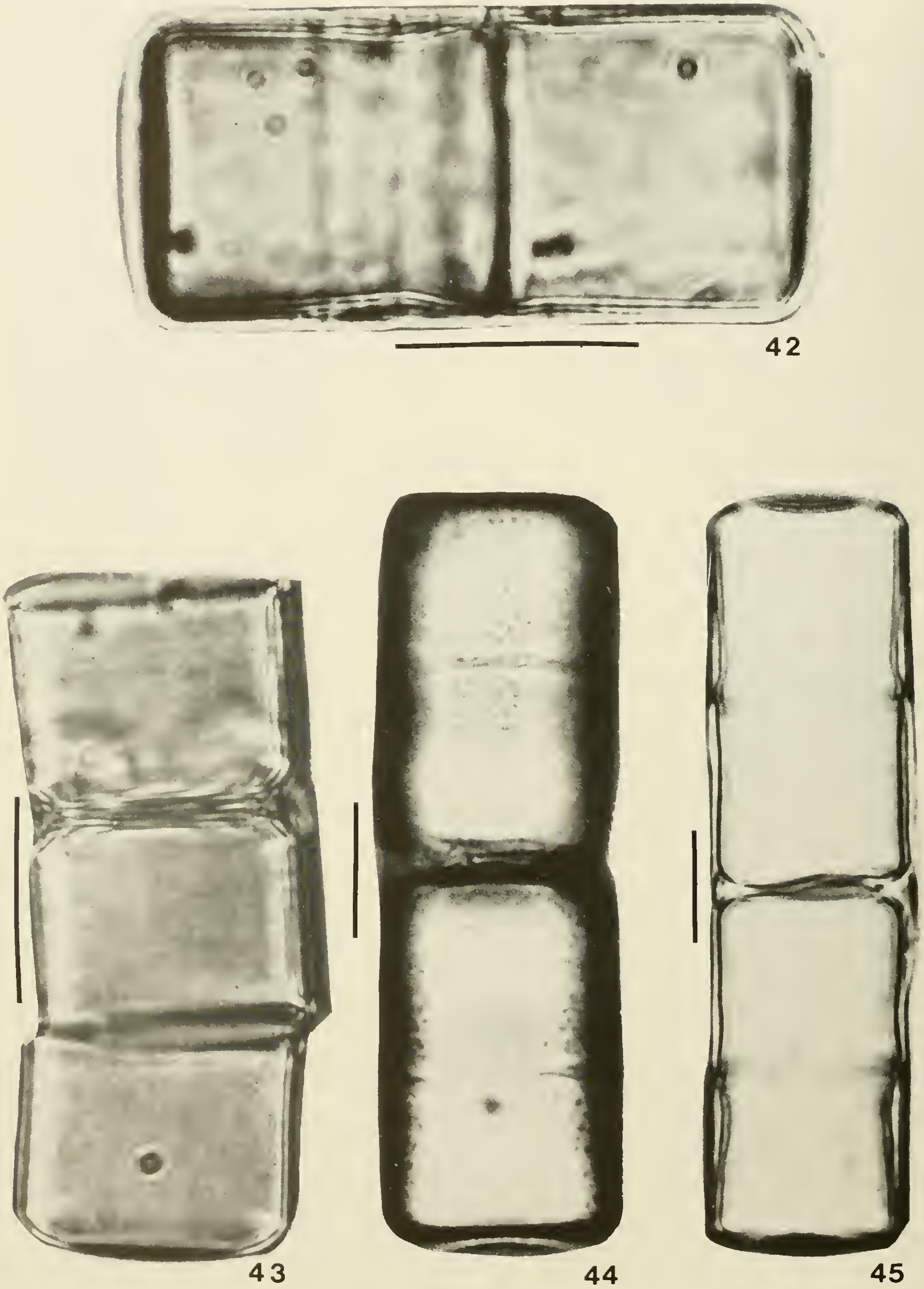
Ecology: alkaliphilous, oligohalobus (indifferent), periphytic (Lowe 1974), mesotrophic, mesohalobus, oligosaprobic (Van der Werff 1957).

Melosira undulata (Ehr.) Kützing

Fig. 41

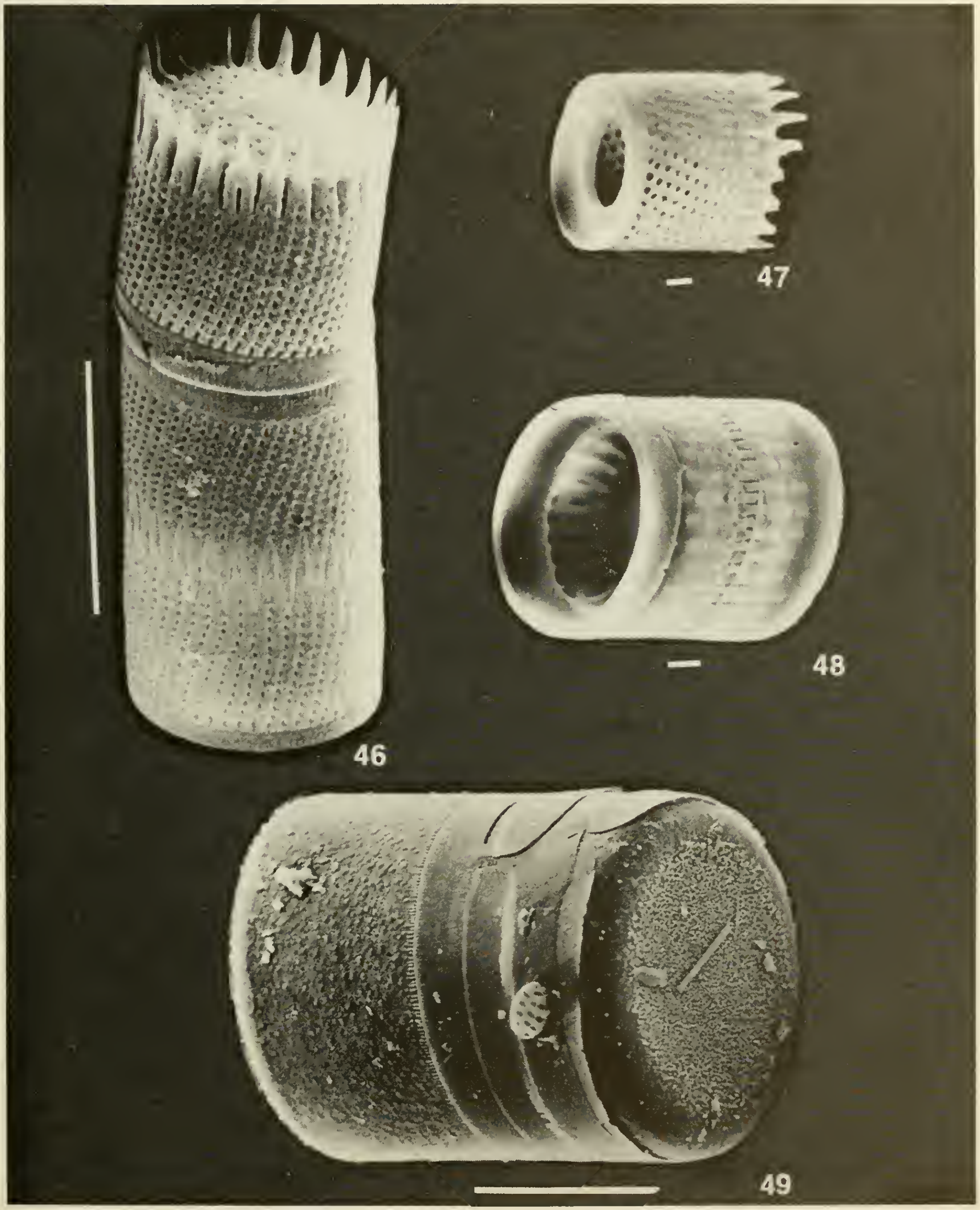
Reference: Hustedt 1927: 243, Fig. 102.

The cells are cylindrical, valve mantle parallel, with a flat valve face forming a very small pseudosulcus. The mantle ornamentation is composed of parallel fine punctae arranged along the pervalvar axis. Conspicuous mucous pores form a ring one-fourth to one-third the distance between the valve and the girdle edge. Although the external mantle walls are parallel, the inner surface of the wall is clearly undulated (Fig. 41). The undu-



Figs. 42–45. *Melosira varians*, girdle views. Scale = 10 μm. LM.

lation is seen as a varying thickness of the wall, with the thickest portion about two-thirds below the valve face. Hustedt (1927) found this species to have a diameter of 16–18 μm and a mantle height of 20–35 μm. *M. varians* C. A. Agardh appears to be sim-



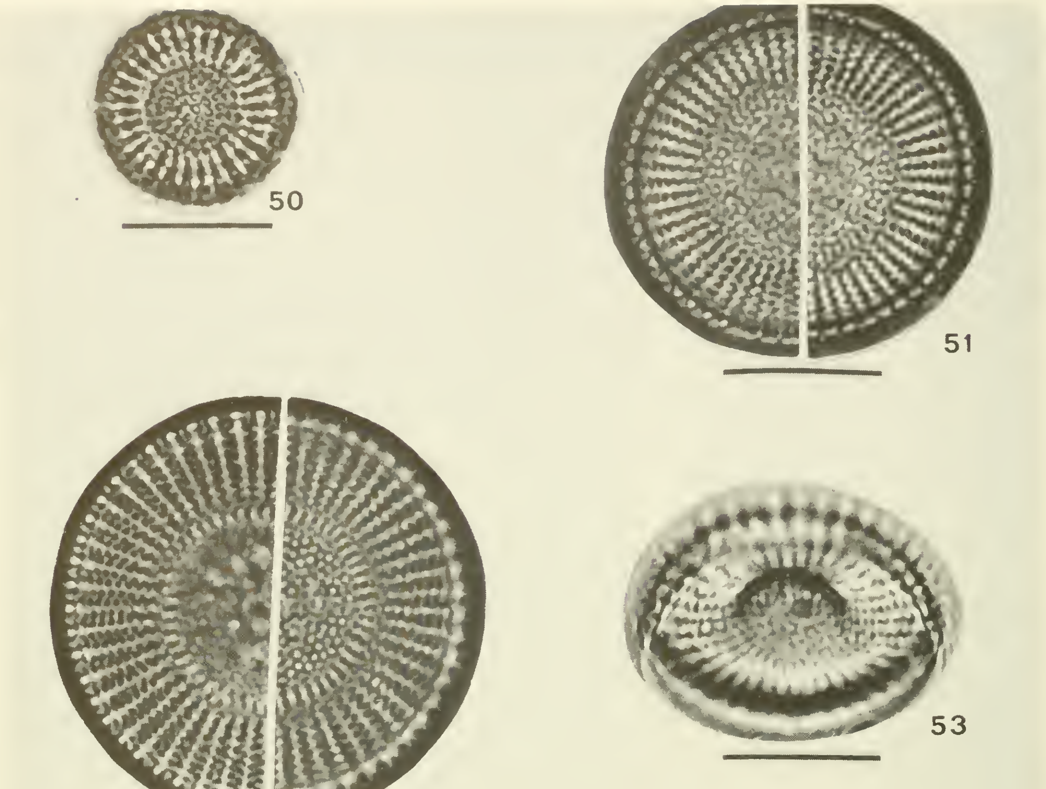
Figs. 46–49. *Melosira italica* (SEM): 46, girdle and valve view (scale = 10 μm); 47, same, view of sulcus (scale = 1 μm); 48, *M. distans* var. *alpigena, view of sulcus and spatulate spines (scale = 1* μm); 49, *M. varians*, girdle and valve view, copulae (scale = 10 μm).

ilar, although the thickening is much reduced and lacks the mantle ornamentation of *M. undulata.*

Distinguishing characteristics: large size and distinctive parallel punctae.

Distribution in Lake Tahoe: infrequent in plankton.

Ecology: oligotrophic (Cleve-Euler 1951).



Figs. 50–55. *Stephanodiscus* spp.: 50, valve view; 51, 52, same, left side focused on margin, right side focused on central area; 53, same, three-fourths view of convex valve; 54, same, girdle view of recently divided cell; 55, *S. carconensis*, valve view, left side focused on central area, right side focused on margin.

Melosira varians C. A. Agardh

Figs. 42–45,49

References: Hustedt 1930: 85, Fig. 41; Cleve-Euler 1951: 29, Fig. 20. CAS No. 60950.

The cells are cylindrical, valve mantle parallel, valve face flat with a very inconspicuous pseudosulcus. The much-reduced pseudosulcus gives the appearance of a homogenous wall thickness. The ornamentation of the valve face and the irregular fine punctae of the mantle can only be resolved with difficulty, using the light microscope. The valve diameter varies from 13–29 μm.

Distinguishing characteristics: rectangular shape in girdle view and the lack of visible ornamentation.

Distribution in Lake Tahoe: infrequent.

Ecology: alkaliphilous, eutrophic, oligohalobus (indifferent). Mesosaprobic, periphytic (Lowe 1974).

Stephanodiscus alpinus Hustedt

Figs. 50–54,56–58

References: Hustedt 1930: 110, Fig. 86; Cleve-Euler 1951; 53, Figs. 70e,f. CAS No. 60951.

The cells are cylindrical with concentrically undulating valves. The valve face is concave or convex, 10–29 μm in diameter (Figs. 56,58). The strong radial striae are separated by a very narrow hyaline rib, with 8–11 ribs in 10 μm at the margin. The marginal striae are composed of three rows of fine areolae, 18–20 areolae in 10 μm (Fig. 56) to about one-third the radius, where they become either bipunctate or unipunctate to the center of the valve. The marginal striae have a zigzag appearance under the light microscope (Figs. 51,52). The marginal spines are located at the junction of the hyaline rib and the mantle, with one spine per rib. Strutted processes are irregularly arranged on the mantle just below the marginal spines. The mantle (Figs. 56,58) is finely punctate up to the radial striations, without the separating hyaline area as reported by Stoermer and Yang (1969).

A comparison of the major morphological structures were made between the species originally designated as *Stephanodiscus astraea* var. *minutula* (Kutz.) Grunow from Lake Tahoe material and *Stephanodiscus alpinus* Hustedt and Ruttner from Grundlsee (Mahood 1978). The measurements taken on Lake Tahoe material compared more closely to the samples and descriptions of *S. alpinus* by Stoermer and Yang (1969) and Huber-Pestalozzi (1942). An extensive discussion of the *S. astraea* var. *minutula*–*S. alpinus* question by Theriot and Stoermer (1982) substantially agrees with our findings. In our examination of Hustedt's slide number 7, from the H. E. Sovereign collection (Mahood 1978), it appears that, when the diameter of the *Stephanodiscus* has a range of 10–17 μm, there is one spine at the end of each rib and the central area is irregular. When the diameter is 19–45 μm the arrangement of the spines is irregular and the central area is radial. When *Stephanodiscus* from Lake Tahoe and *S. alpinus* from Hustedt's slide number 10 from the Sovereign collection were compared to the smaller *Stephanodiscus* on Hustedt's slide 7, we concluded that in each case the measurements match the description for *S. alpinus.*

Distinguishing characteristics: strong radial striations and marginal spines at the end of each rib.

Distribution in Lake Tahoe: common.

Ecology: alkalibiontic, oligohalobus (indifferent), euplanktonic (Lowe 1974), eutrophic (Stoermer and Yang 1969).

Stephanodiscus carconensis Grunow

Fig. 55

References: DeToni 1894; Schmidt 1901; Pl. 228, Figs. 5–6,9–10. CAS No. 60952.

The cells are disk shaped, approximately 49 μm in diameter. There are 15 striae in 10 μm at the margin, with 5–7 striae between thickened hyaline ribs. The central area is granular. The marginal areolae extend toward the central area to form hyaline riblike structures. The spines are submarginal.

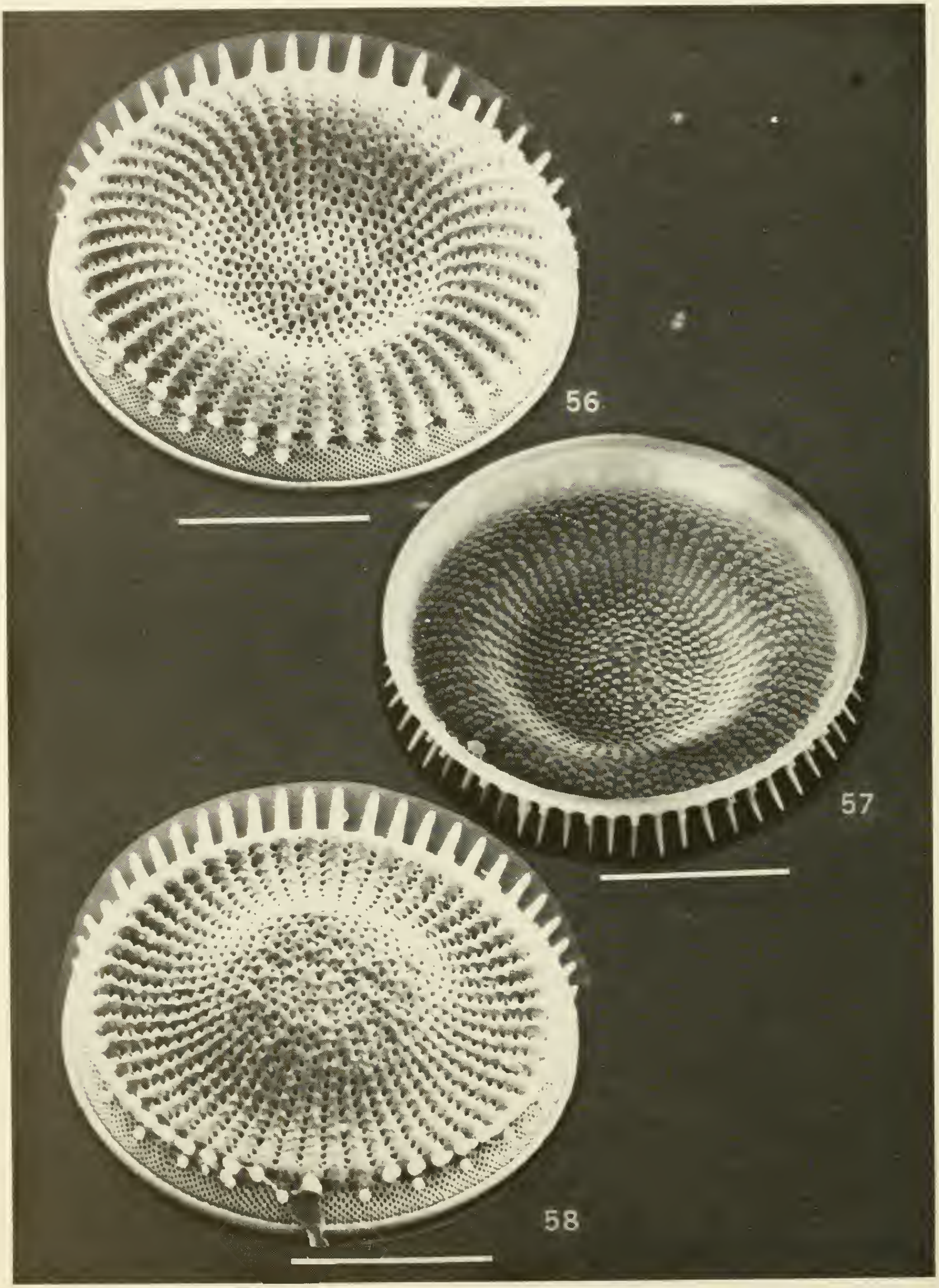
This species is typically thought to be a fossil form. However, Elmore (1921) reported this species in the living state from Devil's Lake, North Dakota. It is also reported alive in Biwa Lake, Japan (Skvortzow 1936). It is difficult to justify the inclusion of *S. carconensis* in the Lake Tahoe algal community on the basis of the collection of a single valve, and its presence is simply noted.

Distinguishing characteristics: very pronounced hyaline ribs and granular central area.

Distribution in Lake Tahoe: very rare.

Discussion

Light microscopy and scanning electron microscopy photographs are presented to aid



Figs. 56–58. *Stephanodiscus alpinus*: 56, external view of concave valve showing spines at margin of each rib; 57, internal view of valve, strutted processes beneath spines, convex; 58, external view of convex valve. Scale = 10 μm. SEM.

in the identification of some difficult species. It is not our intent to rely on SEM as a means of species identification, but rather as a technique that can assist the light microscopist in pragmatic investigations involving some of the more important species.

The denticulate structure of *Melosira italica* are seen as sharp, well-defined spines, whereas the corona of *M. distans* var. *alpigena* can be seen as spatulate ended spines (Figs. 46,48). The coronal structures of *M. distans* var. *alpigena* are extremely difficult to resolve even under optimum conditions of light microscopy. In this case the SEM photographs may assist the investigator in a more accurate separation of these species in initial investigations of the community.

The very small forms of *Cyclotella stelligera* range from 3.5–10 μm in diameter and present the light microscopist with a most difficult task. The characteristics of *C. stelligera*, a stellate central area and central areola, are only positively verified under optimum conditions. For original positive identification within a community, *C. stelligera* must be cleared and mounted in Hyrax or other appropriate high refractive index medium. The SEM photographs of this species (Fig. 14–15,17) have given additional and confirming information, especially regarding the silicified auxospore or initial cell (Anonymous 1975).

Of particular importance are the SEM photographs of the initial cell forms of both *Cyclotella stelligera* (Figs. 14–15,17) and *C. comta* (Figs. 28–29). In light microscopy the initial cell of *C. stelligera* does not resolve well, making identification based on the stellate central area almost impossible. Since the initial cell is almost spherical, the problem is further complicated by depth of field. The SEM photograph of *C. stelligera* (Fig. 17) shows the imperfectly formed central area while clearly showing the development of the alveolate striae.

The SEM photographs of the initial cell form of *C. comta* (Figs. 28–30) may offer a partial solution to the continuing discussion of *C. comta*–*C. bodanica* complex in that the initial cell of *C. comta* resembles *C. bodanica* in the length of the marginal striae. From the SEM photographs the apparent difference, length of striae, between the two may be due to the spherical shape (Fig. 28), poor development of the striae (Fig. 30), and the accompanying difficulties with depth of field when the initial cell is viewed with the light microscope. The characteristics, marginal striae half the radius, of *C. comta* are seen in the vegetative cell (Figs. 22–27) but not in the initial cell forms. The evidence seems to indicate that *C. comta* is the acceptable identification for the morphological characteristics ascribed to *C. comta* in Hustedt (1930).

To ensure consistent and accurate identification of species treated in this paper, individual centered, mounted specimens were verified by the following diatom taxonomists: G. Collins and B. McFarland, United States Environmental Protection Agency, Cincinnati, Ohio; S. Van Landingham, Cincinnati, Ohio; C. L. Christensen, Iowa Academy of Sciences, Waterloo, Iowa; E. F. Stoermer, University of Michigan, Ann Arbor, Michigan; R. Firth, Seaforth, England.

Acknowledgments

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Literature Cited

Anonymous, 1975. Proposals for a standardization of diatom terminology and diagnoses. Nova Hedwigia, Beih. 53:323–354.

Cleve-Euler, A. 1951. Die Diatomeen von Schweden und Finnland. Kungl. Svenska Vet. Akad. Handling. Fjarde Serien. Bd. 2(1):163.

De Toni, G. B. 1894. Sylloge algarum omnium hucusque cognitarum. Pages 818–1556 *in* Vol. 2, Bacillarieae, Sec. 3 Cryptoraphideae. Typis Seminarii, Patavii.

Elmore, C. J. 1921. The diatoms (Bacillarioideae) of Nebraska. University Studies. Univ. of Nebraska 21(1-4-214):22–214.

Goldman, C. R. 1974. Eutrophication of Lake Tahoe emphasizing water quality. EPA-66-/3-74-034. U.S. Govt. Printing Office, Washington, D.C. 408 pp.

Goldman, C. R., M. D. Morgan, S. T. Threlkeld, and N. Angeli. 1979. A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada. Limnol. Oceanogr. 24(2):289–297.

Hanna, G. D. 1930. Hyrax, a new mounting medium for diatoms. J. Roy. Microsc. Soc. Ser. 3, 50(4):422–425.

Hendey, N. I. 1964. An introductory account of the smaller algae of British coastal waters. Part V: Bacillariophyceae. Fishery Investigations Series IV. Her Majesty's Stationary Office, London.

Huber-Pestalozzi, G. 1942. Das Phytoplankton des Süsswassers. Systematik und Biologie: August Thienemann, Die Binnengewässer. E. Schweizerbart 'sche Verlagsbuchhandlung, Stuttgart. Bd. 16, Teil 2 Heft 2, 412 pp.

Hustedt, F. 1927. Die Kieselalgen Deutschlands, Österreichs der Schweig unter Berüchsichtigung der übrigen Länder Europas sowei der angrenzenden Meeresgebiet. Pages 217–273 *in* L. Rabenhorst, ed., Kryptogamen-Flora von Deutschland, Österreich und der Schweig, Bank 7, Teil 1.

______. 1930. Bacillariophyta (Diatomeae). *In* A Pascher, Die Süsswasser-Flora Mitteleuropas, Heft 10, 2 Auflage Gustav Fisher, Jena. 466 pp.

Lowe, R. L. 1974. Environmental requirements and pollution tolerance of freshwater diatoms. U.S. Environmental Protection Agency, EPA-670/4-74-005.

Mahood, A. D. 1978. The Harry E. Sovereign Collection of Northwest Pacific diatoms. Proc. California Acad. Sci., Ser. 4, 41(13):339–343.

Mandra, Y. T., A. L. Brigger, and H. Mandra. 1973. Chemical extraction techniques to free fossil silicoflagellates from marine sedimentary rocks. Proc. California Acad. Sci., Ser. 4, 39(15):273–284.

Meakin, S. H. 1939. How to study diatoms. Microscope. 3:152,187,209,239; 4:8,50.

Pantocsek, J. 1902. A Balaton Kovamosnatai vagy Bacillariái, Balaton tudomanyoa Tarrukman Yozasanak Erednenyei. Budapest. 144 pp.

Patrick, R., and C. W. Reimer. 1966. The diatoms of the United States. I. Monogr. Acad. Nat. Sci. Philadelphia 13:91–97.

Schmidt, A. 1874–1944. Atlas der Diatomaceenkunde (Publications continued by M. Schmidt, Fr. Frick, O. Müller, H. Heiden, and Fr. Hustedt) Aschersleben-Leipzig. Pls. 1–460.

Skvortzow, V. B. 1936. Diatoms from Biwa Lake, Honshu, Nippon. Philippine J. Sci. 61(2):254–296.

Stoermer, E. J., and J. J. Yang. 1969. Plankton diatom assemblage in Lake Michigan. Univ. of Michigan, Great Lakes Research Division. 18050DKC.

Theriot, E., and E. F. Stoermer. 1982. Observations on North American populations of Stephanodiscus (Bacillariophyceae) species attributed to Fredrich Hustedt. Trans. Amer. Microsc. Soc. 101(4):368–374.

Tilzer, M. M., and C. R. Goldman. 1978. Importance of mixing and thermal stratification for phytoplankton productivity in Lake Tahoe (California-Nevada). Ecology 59(4):810–821.

Van der Werff, A. 1955. A new method of concentrating and cleaning diatoms and other organisms. Proc. Internat. Assoc. Theor. Appl. Limn. 1:276–277.

Van der Werff, A. en Huls. 1957. Diatomeeenflora van Nederland. Abcoude, Den Haag.

Van Heurck, H. 1896. A treatise on the Diatomaceae. William Wesley and Sons, London. 558 pp.

Van Landingham, L. S. 1967. Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Verlag von J. Cramer, Lehrer. Part I, pp. 1–496.

______. 1969. Catalogue of the fossil and recent genera and species of diatoms and their synonyms. Verlag von J. Cramer, Lehrer. Part II, pp. 497–1086.

DISTRIBUTION OF SHORE BUGS AND SHORE FLIES AT SYLVAN SPRINGS, YELLOWSTONE NATIONAL PARK

Vincent H. Resh[1] and Mark A. Barnby[1]

Abstract.— Three species of shore bugs (Hemiptera: Saldidae) and 10 species of brine flies (Diptera: Ephydridae) were collected at Sylvan Springs (Wyoming section of Yellowstone National Park, USA), an area containing both acid and alkaline thermal springs. The fauna consists of both widespread (e.g., shore bugs *Saldula comatula* Parshley and *Saldula explanata* [Uhler] and shore flies *Atissa litoralis* [Cole] and *Scatella stagnalis* [Fallén]) and Yellowstone Park–endemic species (e.g., *Saldula* nr. *arenicola* and the shore fly *Ephydra thermophila* Cresson). The ratio of adults to nymphs of the numerically dominant shore bug *Saldula* nr. *arenicola* is higher along heated margins (11–12:1) than along near-ambient-temperature margins (0.6–2:1) of a thermal channel at Sylvan Springs; this may reflect differences in food availability, osmoregularity, thermal tolerance, predation, or other factors. Shore flies include species typical of acid (*E. thermophila*) and alkaline (*Paracoenia bisetosa* [Coquillett] and *Paracoenia turbida* [Curran]) springs.

The insect fauna of thermal springs has been of interest to biologists worldwide (Tuxen 1944, Winterbourn 1968), but most attention in North America has been focused on the inhabitants of thermal areas in Yellowstone National Park (Montana, Idaho, but mainly Wyoming, USA). Early studies by Brues (1924, 1932) on the distribution of insects in Yellowstone thermal springs examined the faunal diversity of such habitats, and more recent studies such as Wiegert and Mitchell (1973), Collins (1975), and Collins et al. (1976) have shown that such habitats are useful field laboratories for examining conceptual aspects of insect ecology.

In Yellowstone Park hot springs, the distribution of at least some species of shore flies (Diptera: Ephydridae) may be related to the pH of these spring habitats (Wirth 1971). Since Sylvan Springs is an area of the Park that contains both alkaline and acid springs, the fauna was examined to determine whether insect species described as typical inhabitants of acid, alkaline, or both spring types occur in this area.

Methods

Brock (1978, Table 2.3) reported the water chemistry of 12 of the many springs that comprise Sylvan Springs. Two of these 12 springs were alkaline (pH values of 7.2 and 8.3), whereas the remaining 10 were acidic (pH of 1.8–5.3). At Sylvan Springs the green alga *Cyanidium caldarium* occurs in the outflows of acidic springs at pH$<$4, and it is the sole photosynthetic organism inhabiting spring outflows where temperatures are between 40 and 57 C (Brock 1978). A large mat of the green alga *Zygogonium* is also present at Sylvan Springs (Lynn and Brock 1969). Although this mat is adjacent to thermal areas, the water temperatures in the mat are close to those of ambient air.

Shore bugs (Hemiptera: Saldidae) and shore flies (Diptera: Ephydridae) were collected on 16 August 1982 from the periphery of the *Zygogonium* mat and along the margins of the main channel into which many of the springs at Sylvan Springs flow. Along this channel, which is approximately 150 m in length, water temperature ranged from below that of ambient air (which was 27 C at time of collections) up to 54 C. The area in which all collections were made is described by Brock (1978, Fig. 2.4, the lower quarter of the map); approximately 500 m^2 of habitat was sampled.

Results

Shore Bugs

Although the saldid *Micracanthia quadrimaculata* (Champion) has been reported to be abundant on and around the *Zygogonium* mats of Yellowstone Park acid springs (Collins 1972), we did not collect this species on this algal mat or in any other area of Sylvan Springs. Instead, the numerically dominant shore bug was an undescribed species of *Saldula*, in the *arenicola* group of this genus. This species appears to be endemic to thermal springs, and possibly to Yellowstone Park (J. T. Polhemus, unpubl. data). Since the entire *arenicola* group requires taxonomic revision (J. T. Polhemus, pers. comm.), this species will not be described here.

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Two other species of shore bugs were collected at Sylvan Springs, *Saldula comatula* Parshley and *Saldula explanata* (Uhler). Both species are widely distributed throughout the western U.S. and Canada (Polhemus and Chapman 1979).

Within the Sylvan Springs area, S. nr. *arenicola* occurs on the ambient-temperature *Zygogonium* mat and along the margins of the main thermal channel. Individuals of this species that occur along the channel margins where water temperature is above 40 C die if they fall into the heated water. This species is unusually slow moving compared to most species of Saldidae, and a similar "sluggishness" has been reported for *Saldula usingeri* Polhemus from a California thermal spring (Polhemus 1967). This behavior may be an adaptation to avoid accidentally landing in lethal thermal waters.

The distribution of nymphs and adults of S. nr. *arenicola* varies along the thermal gradient of the main Sylvan Springs channel. The ratio of adults to nymphs is 11:1 where water temperature is 54 C and 12:1 at 42 C. In contrast, at temperatures of 30 C the ratio is less than 2:1, at 27 C it is 1:1, and at 24 C it is 0.6:1.

Saldula comatula and S. *explanata* did not occur along the thermal portions of the channel that were occupied by S. nr. *arenicola*. Both species were limited to the ambient temperature areas of the channel that were near the juncture of Sylvan Springs with the surrounding meadow and forest areas.

Shore Flies

Ten species of Ephydridae were collected at Sylvan Springs (Table 1). Eggs, larvae, and pupae of *E. thermophila*, the only ephydrid collected in the *Zygogonium* mat, were found in small pools of spring water; these ambient-temperature pools were approximately 1–3 cm deep and had no discernible flow. In contrast, Collins (1975) reported that high densities of *E. thermophila* eggs and larvae only occurred in the portions of a *Zygogonium* mat that were near outflows with high temperatures and concentrations of interstitial algae.

Adults of only 3 shore fly species, *E. thermophila*, S. *stagnalis*, and *A. litoralis*, occurred along the heated margins of the main channel, although all 10 shore fly species listed in Table 1 occurred along margins where water temperature was near that of ambient air. The above-named three species together comprised almost 90% of all shore flies collected (Table 1); this was, at least in part, because their distribution covered more of the areas of Sylvan Springs that we examined.

Since Sylvan Springs is used by park naturalists in their interpretive programs, the immature stages of shore flies within the thermal effluents were not quantitatively collected because such sampling would drastically alter the appearance of this habitat. However, the four benthic collections that were made indicated that far more shore fly larvae and pupae occurred in the cooler than in the heated portions of Sylvan Springs.

DISCUSSION

The shore bug and shore fly components of the Sylvan Springs fauna consist of some species that are apparently endemic to Yellowstone Park (e.g., S. nr. *arenicola*, *E. thermophila*), and others that are more widespread in their distribution (e.g., S. *explanata*, S. *stagnalis*). The shore bug *M. quadrimaculata* that was previously reported as an inhabitant of Yellowstone Park acid springs closely resembles *Saldula* spp. in appearance and may have been misidentified in earlier studies.

The changing ratio of S. nr. *arenicola* adults to nymphs along the Sylvan Springs channel in which higher proportions of adults were found in heated areas, but higher proportions of nymphs were found in cooler areas, is similar to a pattern reported long ago by Hubbard (1892) for adults and larvae of the carabid beetle *Nebria* in Yellowstone Park hot spring effluents. Such a pattern could result from factors that favor nymphs in the cooler areas or adults in the heated areas, or factors detrimental to nymphs in the heated areas or adults in the cooler areas.

Increased numbers of nymphs along the cooler margins could result from S. nr. *arenicola* adults selectively ovipositing in areas that contain more abundant food. Collins (1972) described the saldids in these habitats as saprovores, whereas our studies with other species of *Saldula* suggest that they may be at least facultative predators of shore fly larvae. With either type of feeding though, the benthic samples that were made indicate that more potential food sources occur in the cooler areas of the main channel.

Increased numbers of adults along the heated margins could be related to osmoregulative or reproductive activities. For example, sexually active adults of *Saldula saltatoria* L. required high humidity microclimates to counter loss of body water (Lindskog 1968). At Sylvan Springs, higher humidity microclimates occur along the heated spring margins and might influence the distribution of S. nr. *arenicola* adults.

Since food resources are less abundant along the heated margins, adult shore bugs may cannibalize their conspecific nymphs, and consequently reduce the relative abundance of nymphs in these areas. Decreased numbers of nymphs along the heated margins may also reflect different thermal tolerances among nymphal and adult stages. Larvae of the beetle *Nebria* that Hubbard (1892) reported as more abundant in the cooler portions of hot spring effluents probably occur there because of the low thermal tolerance of the larvae (D. H. Cavanaugh, pers. comm.).

Finally, decreased numbers of adults along the cooler margins could result from selective predation by insectivorous birds, such as killdeer, *Charadrius vociferous*, that are resident to Sylvan Springs. Brock and Brock (1968)

Table I. Adult shore flies collected at Sylvan Springs, which is in the Wyoming section of Yellowstone National Park.

Species collected	Total flies collected (%)	Distribution
Atissa litoralis (Cole)	55	Primarily east to midwest, but also in far western U.S. (Sturtevant and Wheeler 1953).
Scatella stagnalis (Fallén)	18	Nearctic and Europe (Sturtevant and Wheeler 1953).
Ephydra thermophila Cresson	14	Endemic to Yellowstone Park: Frying Pan Springs, Norris Annex Hot Springs, Nymph Creek, Sylvan Springs, Mud Volcano Springs (Wirth 1971); Sylvan Springs (Collins 1972, 1975).
Lamproscatella arichaeta Mathis	6	Mainly west of the 100th meridian, between 32° and 49° north latitude (Mathis 1979a); In Yellowstone Park: Upper Geyser Basin (collected in 1916 by A. L. Melander [Mathis 1979a]).
Scatophila sp.	4	Taxonomic difficulties in group preclude further identification of species.
Paracoenia bisetosa (Coquillett) and *Paracoenia turbida* (Curran)	1	Both species primarily in western North America (Mathis 1975); In Yellowstone Park: (localities may refer to either or both species) Lower Geyser Basin (Brock et al. 1969, Wiegert and Mitchell 1973, Collins 1977, Kuenzel and Wiegert 1977); Nez Percé Spring (Collins et al. 1976).
Scatella paludum (Meigen)	1	Holarctic; In Yellowstone Park: Sylvan Springs (Collins 1972, 1977).
Discocerina obscurella (Fallén)?	<1	Species is Holarctic, but taxonomic difficulties in group preclude positive identification of species.
Notiphila decoris Williston	<1	Mainly west of the 100th meridian, from Manitoba southward into Mexico (Mathis 1979b); In Yellowstone Park: Old Faithful, Upper Geyser Basin, West Thumb Geyser Basin, White Dome Geyser vicinity (Mathis 1979b).

noted that killdeer catch and feed on insects that occur on algal mats in cooler portions of thermal habitats. These birds may feed more heavily on the larger, more active adults of S. nr. *arenicola* than on the nymphs.

There are other possible causes of the observed pattern as well. Age-specific, diurnal, or seasonal migrations may occur in relation to this gradient, and these movements could produce such a distribution. However, additional research is needed to demonstrate which of the above, or if other, unmeasured, factors were responsible for the pattern observed.

The shore fly fauna of Sylvan Springs includes species that have been reported from either only acid (e.g., *E. thermophila*) or only alkaline (e.g., *P. bisetosa* and *P. turbida*) springs. Some confusion in the identification of these two species of *Paracoenia* in Yellowstone studies has lead to difficulties in interpreting the results of previously published research (Wirth and Mathis 1979), but both species have been reported as occurring in alkaline habitats (Wirth and Mathis 1979, Table 2). The relative abundance of acid-spring and alkaline-spring species at Sylvan Springs (e.g., *E. thermophila* 14%, *Paracoenia* spp. 1%, Table 1) reflects the pattern that acid springs are more common than alkaline springs in this habitat.

Acknowledgments

We thank J. T. Polhemus and W. N. Mathis for confirming shore bug and shore fly identifications, T. D. Brock for supplying information on the water chemistry of Sylvan Springs, and D. H. Cavanaugh for his comments on *Nebria* biology. This research leading to this report was supported in part by the United States Department of the Interior, under the Annual Cooperative Program of Public Law 95-467, Project A-084-CAL, and by the University of California Water Resources Center, Project UCAL-WRC-W-612.

Literature Cited

Brock, T. D. 1978. Thermophilic microorganisms and life at high temperatures. Springer-Verlag. New York. 465 pp.

Brock, T. D., and M. L. Brock. 1968. Life in a hot-water basin. Nat. Hist. 77:47–54.

Brock, M. L., R. G. Wiegert, and T. D. Brock. 1969. Feeding by *Paracoenia* and *Ephydra* (Diptera: Ephydridae) on the microorganisms of hot springs. Ecology 50:192–200.

Brues, C. T. 1924. Observations on animal life in the thermal waters of Yellowstone Park, with a consideration of the thermal environment. Proc. Amer. Acad. Arts Sci. 59:371–437.

______. 1932. Further studies on the fauna of North American hot springs. Proc. Amer. Acad. Arts Sci. 67:185–303.

Collins, N. C. 1972. Population biology of the brine fly *Ephydra thermophila* (Diptera: Ephydridae) associated with acid seepages in Yellowstone National Park, Wyoming. Unpublished dissertation, Univ. of Georgia, Athens, Georgia. 50 pp.

______. 1975. Population biology of a brine fly (Diptera: Ephydridae) in the presence of abundant algal food. Ecology 56:1139–1148.

______. 1977. Mechanisms determining the relative abundance of brine flies (Diptera: Ephydridae) in Yellowstone thermal springs effluents. Can. Entomol. 109:415–422.

Collins, N. C., R. Mitchell, and R. G. Wiegert. 1976. Functional analysis of a thermal spring ecosystem, with an evaluation of the role of consumers. Ecology 57:1221–1232.

Hubbard, H. G. 1892. Insect life in the hot springs of the Yellowstone National Park. Can. Entomol. 23:226–230.

Kuenzel, W. J., and R. G. Wiegert. 1977. Energetics of an insect predator, *Tachytrechus angustipennis* (Diptera). Oikos 28:201–209.

Lindskog, P. 1968. The relations between transpiration, humidity reaction, thirst and water content in the shore bug *Saldula saltatoria* L. (Heteroptera: Saldidae). Arkiv Zool. 20:465–493.

Lynn, R., and T. D. Brock. 1969. Notes on the ecology of a species of *Zygogonium* (Kütz) in Yellowstone National Park. J. Phycol. 5:181–185.

Mathis, W. N. 1975. A systematic study of *Coenia* and *Paracoenia* (Diptera: Ephydridae). Great Basin Nat. 35:65–85.

______. 1979a. Studies of Ephydrinae (Diptera: Ephydridae), II: phylogeny, classification, and zoogeography of nearctic *Lamproscatella* Hendel. Smithson. Contrib. Zool. 295:1–41.

______. 1979b. Studies of Notiphilinae (Diptera: Ephydridae), I: Revision of the nearctic species of *Notiphila* Fallén, excluding the *caudata* Group. Smithson. Contrib. Zool. 287:1–111.

Polhemus, J. T. 1967. A new saldid from California (Hemiptera: Saldidae). Proc. Entomol. Soc. Washington 69:346–348.

Polhemus, J. T., and H. C. Chapman. 1979. Family Saldidae/shore bugs. Pages 16–33 *in* A. S. Menke, ed., The semiaquatic Hemiptera of California (Heteroptera: Hemiptera). Bull. California Insect Surv. 21:1–166.

Sturtevant, A. H., and M. R. Wheeler. 1953. Synopses of Nearctic Ephydridae (Diptera). Trans. Amer. Entomol. Soc. (Philadelphia) 79:151–261.

Tuxen, S. L. 1944. The hot springs of Iceland. Their animal communities and their zoogeographical significance. Einar Munksgaard, Copenhagen, Denmark. 216 pp.

WIEGERT, R. G., AND R. MITCHELL. 1973. Ecology of Yellowstone thermal effluent systems: intersects of blue-green algae, grazing flies (*Paracoenia*, Ephydridae) and water mites (*Partnuniella*, Hydrachnellae). Hydrobiologia 41:251–271.

WINTERBOURN, M. J. 1968. The faunas of thermal waters in New Zealand. Tuatara 16:111–122.

WIRTH, W. W. 1971. The brine flies of the Genus *Ephydra* in North America (Diptera: Ephydridae). Ann. Entomol. Soc. Amer. 64:357–377.

WIRTH, W. W., AND W. N. MATHIS. 1979. A review of Ephydridae living in thermal springs. Pages 21–46 *in* D. L. Deonier, ed., First symposium on systematics and ecology of Ephydridae (Diptera). North American Benthological Society, Erie, Pennsylvania. 147 pp.

SIZE AND SEASONAL ACTIVITY PATTERNS OF ABUNDANT SYMPATRIC SPIDER SPECIES IN CACHE COUNTY, UTAH

James V. Robinson[1]

ABSTRACT.— Of the eight most frequently collected spiders at a northern Utah study site, each of two species employed one of the following hunting strategies: pursuing, web building, jumping, and ambushing. Within each pair, size differences between species were substantial for all but the ambushers. The ambushers had different seasonal activity patterns, as did the web builders.

Spider species may have very broad food preferences (Savory 1928, Turnbull 1960, Riechert 1974, Jackson 1977) yet still obtain different types of prey because of seasonal activity patterns, size differences, habitat preferences, and hunting strategies. The persistence of spider species assemblages at a given site over a period of time may depend on combinations of such differences being sufficient to reduce interspecific competition. This report documents the seasonal activity and size patterns of the eight most frequently collected spider species at a northern Utah study site near Logan and makes comparisons between those species having the most similar hunting strategies.

It is difficult to evaluate what minimal separation in resource utilization is required for species coexistence in natural environments. Most theoretical considerations of this question have involved mathematical analyses of models in which species are competing for a single resource along a continuum (May and MacArthur 1972, May 1973, Roughgarden 1979). These analyses suggest that such species can coexist if the means of their resource use, along the continuum, are separated by an amount larger than the standard deviation of their resource use. Prey size is a frequently considered resource continuum. Because of the difficulty of obtaining data regarding actual diet, inferences are often made regarding prey size separation based on the relative sizes of the competing predators. This approach originated from the observations of Hutchinson (1959) on corixid insects and his tabulation of data concerning birds and mammals. He concluded that sympatric species having similar ecological requirements are separated by an average ratio of 1.28 (range 1.1 to 1.4) for linear body measurements correlated with feeding. More recent support for this notion came from May (1973), who argued that competing sympatric predators must have their linear dimensions separated by a ratio of 1.2 to 1.4 for them to successfully coexist within a single resource continuum. Hutchinson (1959) also argued that organisms that must obtain their own nourishment throughout life unaided by parents and that also have annual life cycles are under different selective pressure than those that only procure food unaided at or near their adult size. He hypothesized that coexistence of the former type of species required the larger of the two species to begin its development prior to the smaller species. Empirical evidence exists for such relationships among some spiders (Enders 1976, Uetz 1977, Peck and Whitcomb 1978).

Considerable variation exists in the hunting strategies used by spiders (Gertsch 1949, Kaston 1948). This may influence the susceptibility to capture of different prey types, which may be reflected in spider community composition (Balogh and Loska 1974 in Turnbull 1973, Enders 1975, Uetz 1977, Hatley and MacMahon 1980, Robinson 1981). Al though these strategies may be divided into a number of small categories, Robinson (1981) found it useful to lump the spiders considered here into four guilds: pursuers, ambushers,

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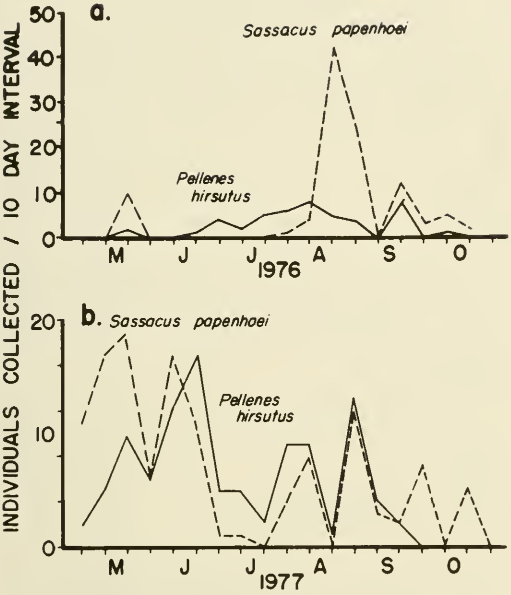

Fig. 1. Numbers of individuals of the two dominant jumping species collected per 10-day interval plotted against date for 1976 and 1977.

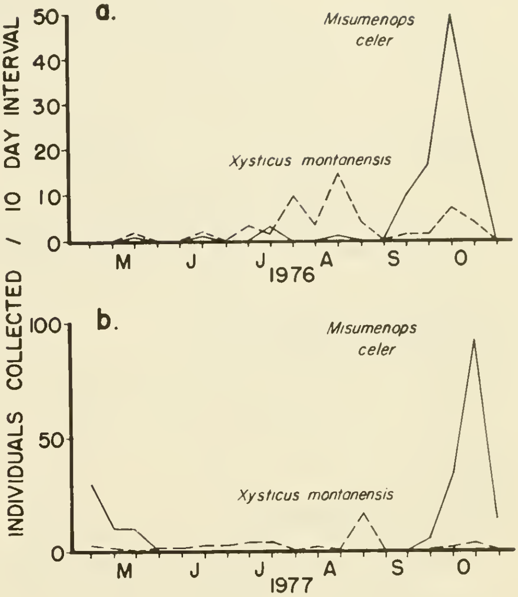

Fig. 2. Numbers of individuals of the two dominant ambushing species collected per 10-day interval plotted against date for 1976 and 1977.

jumpers, and web builders; this procedure is followed in this paper.

The spectrum of prey encountered by a spider species is also related to the temporal patterns of abundance and activity of that spider species. Uetz (1975) found that seasonal species richness of spiders was strongly correlated with the seasonal pattern of insect abundance. He suggested that increased prey abundance was accompanied by more niche overlap for spiders; hence more species of spiders could temporally fit into the community. Tretzel (1955), Uetz (1975), and Peck and Whitcomb (1978) also report that temporal variation is an important factor in spider coexistence.

Hatley and MacMahon (1980) and Robinson (1981) suggest that spiders may partition the vegetation in ways that improve the hunting efficiency of certain species. Jumping spiders were shown to prefer open habitat, and web building spiders of the genus *Theridion* preferred dense habitat. Other microhabitat preferences in spiders have been reported (e.g., Duffey 1962, Judd 1965, Enders 1974, Greenquist and Rovner 1976).

Some attributes of a spider community near Green Canyon, Cache County, Utah, were determined to evaluate their potential importance as coexistence mechanisms. Data pertaining to juvenile emergence dates, seasonal activity abundances, and seasonal patterns of body lengths are here presented.

METHODS

A spider community was sampled by collecting all individuals present on modular habitat units left in the field for a predetermined time interval (Robinson 1981). These modular habitat units consisted externally of 30.48 cm (1 ft) cubes of 2.54 cm (1 in) mesh chicken wire, and internally of various architectural configurations constructed of 5-ply macrame jute.

All sampling took place on the Bonneville Lake terrace of the Bear River Range, 3.2 km northeast of Logan, Utah, near the mouth of Green Canyon. The site was dominated by big sage (*Artemisia tridentata*) and contained, among other herbaceous species, *Balsamorhiza sagittata* and *Wyethia amplexicaulis* in abundance.

With the exception of several members of the Erigoninae, all spiders collected were identified to species. Species identifications were aided by reference collections developed by Hatley and Abraham and determined by W. Gertsch. Spider body lengths

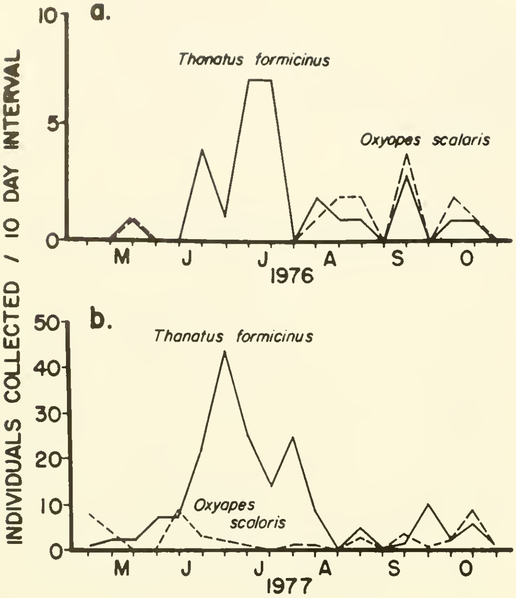

Fig. 3. Numbers of individuals of the two dominant pursuing species collected per 10-day interval plotted against date for 1976 and 1977.

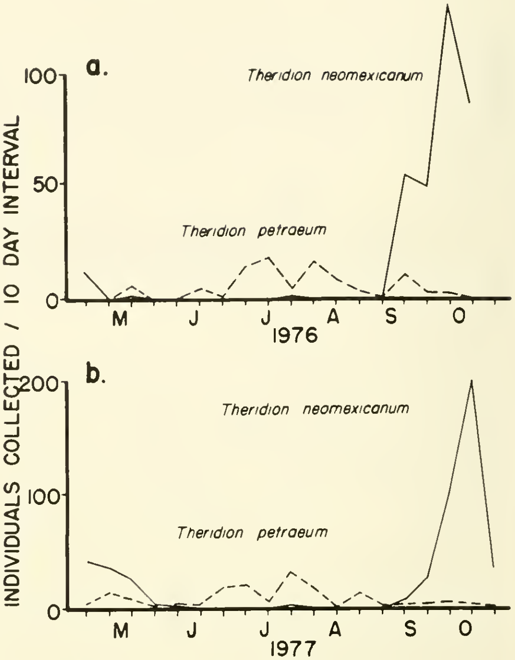

Fig. 4. Numbers of individuals of the two dominant web-building species collected per 10-day interval plotted against date for 1976 and 1977.

were measured using low power on a WILD model M4 binocular microscope fitted with an ocular micrometer; this permitted resolution to approximately 0.07 mm. Spinnerets were not included in measurements.

All species present were *a priori* assigned to one of the following four hunting guilds: pursuers, ambushers, jumpers, or web builders. All species for which more than 50 individuals were collected during the two field seasons studied were considered sufficiently abundant to warrant further analysis.

Data pertaining to the number of individuals collected per 10-day interval and the measured body lengths of the most abundant species were plotted as a function of time. Individuals were separated into two cohorts, assumed to represent animals of the current and previous year. Separation was based on either the presence of adult characteristics or the approximate body size expected for a given date. This latter method has precedence in entomology (Drooz 1965, Enders 1976). Linear regression analyses were then performed on the body length data for each abundant species. The current year's cohorts were separately analyzed for the 1976 and 1977 field seasons, and the previous year's cohorts were analyzed only for 1977 field season (the beginning process in 1976 was sufficiently delayed so that only marginally complete data were obtained). The regressions of body length on a given date were tested for significant nonzero slopes using a standard F-ratio test. Only those sections of the line were graphed (Figs. 5–7) that coincided with the range of collection dates for the cohort. The earliest emergence date for which individuals were collected was thus indicated for each abundant species by the left-most portion of its regression line. To minimize the visual impact of extreme values, the beginning of the second quartile of individuals and the end of the third quartile were marked with brackets on the regression lines (Figs. 5–7). These quartiles refer to the number of individuals, of that cohort, collected during the respective field season.

Results and Discussion

Of the 45 species collected during this research, only 8 were collected in numbers exceeding 50 individuals during the two field seasons. Each of the four major hunting guilds (ambushers, jumpers, pursuers, and

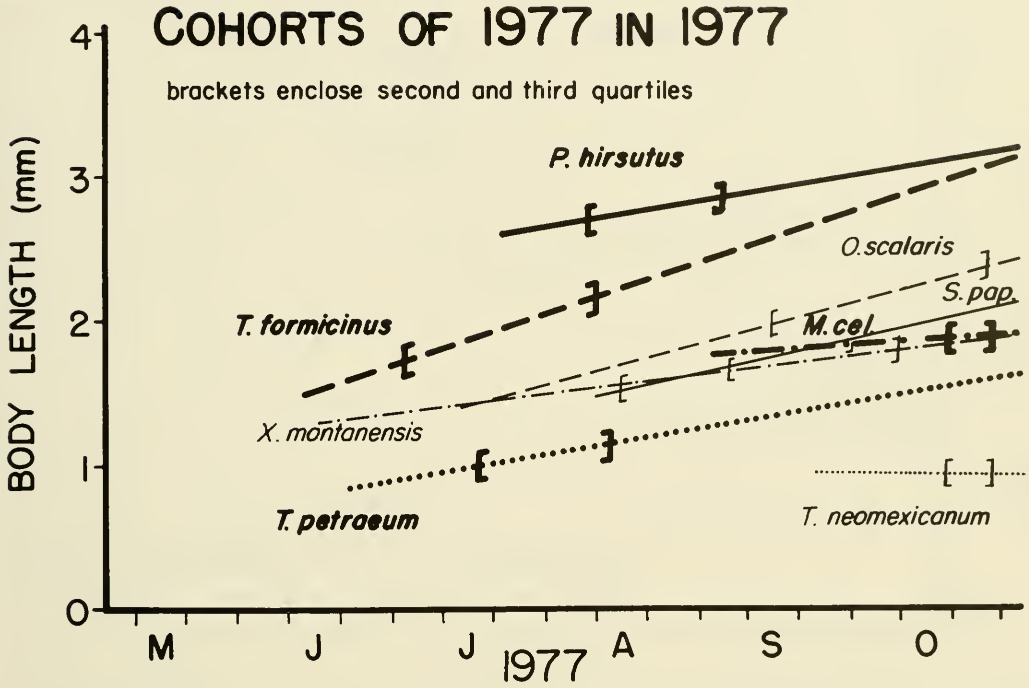

Fig. 5. Body length regression lines for the 1976 cohorts of the eight most abundant spider species collected during the 1976 field season. Solid lines represent jumping species, dashed lines represent pursuing species, dash-dot lines represent ambushing species, dotted lines represent web-building species.

web builders) was composed of a different pair of these abundant species.

The total numbers of each of the abundant species collected during 10 day intervals were plotted against date for each of two field seasons. For comparative purposes, each pair of species having the same hunting strategy was plotted on the same graph. The two jumping species, *Sassacus papenhoei* and *Pellenes hirsutus*, overlap each other seasonally, each occurring in all seasons (Fig. 1). The two ambusher species, *Misumenops celer* and *Xysticus montanensis*, subdivide the field season with *Misumenops* active early and late, and *Xysticus* active more toward midseason (Fig. 2). The pursuers, *Thanatus formicinus* and *Oxyopes scalaris*, occur with considerable overlap (Fig. 3). The web builders, *Theridion neomexicanum* and *T. petraeum*, are separated seasonally: *T. neomexicanum* is active early and late in the season; *T. petraeum* is active in the middle of the season (Fig. 4).

Regression lines representing the body lengths of these abundant species were developed and plotted for each cohort in each field season (Figs. 5–7). The values obtained from these regressions are indicative of the size of organisms collected on different dates. For those species belonging to the same hunting guilds, the minimum ratios separating the pairs were tabulated (Table 1). The larger of the two species (in terms of those adults collected) emerged first as juveniles in each of the two field seasons and for all four species pairs. This was consistent whether the date of emergence measurement was based on the earliest capture or on those species that had the first quartile of their individuals, within that year's cohort, collected first.

The two jumping spiders, although overlapping in seasonal distribution, are different enough in size throughout the year to permit coexistence according to theory. The two pursuers also overlapped each other with regard to seasonal activity, but in this case no significant nonzero regression of size on Julian date was found for adult *Oxyopes* (the smaller of the pair); this may be due to its being the least abundant of these eight species. When the largest one-third of the individuals collected of each pursuer species is

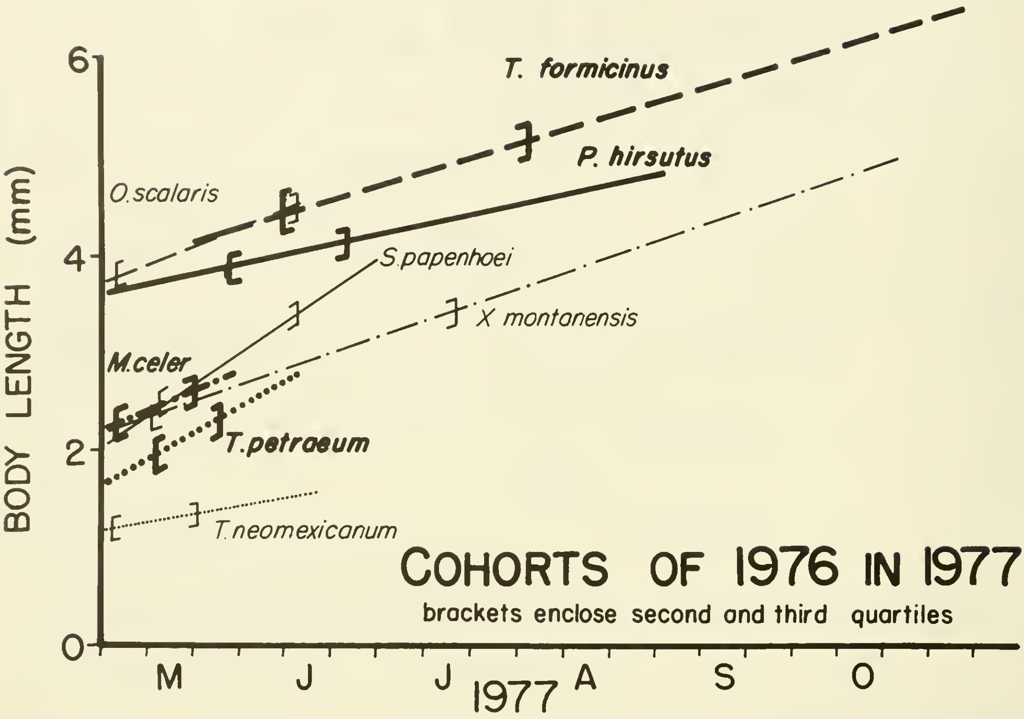

Fig. 6. Body length regression lines for the 1976 cohorts of the eight most abundant spider species collected during the 1977 field season. Hunting strategies are represented by line types described in Figure 5.

compared (Schoener 1970), the ratio of *Thanatus* to *Oxyopes* is 1.23. This suggests that size is also important for these species. The two web builders were both differentiated in size and seasonal activity. Finally, although no clear patterns in size differences were found between ambushers, differential seasonal activity does appear significant. These two species were also observed to use different habitats; *Xysticus* had a prediliction toward stemlike material, and *Misumenops* concentrated on the yellow flowers of *Wyethia* and *Balsamorhiza*.

ACKNOWLEDGMENTS

I thank Drs. Lloyd Bennett, Ronald Canfield, Barrie Gilbert, and Ivan Palmblad for

TABLE 1. Minimum ratios obtained between the body lengths of species cohorts of each hunting guild.

Guilds			Ratio for cohorts of		
Larger species as adult		Smaller species as adult	1976 in 1976	1976 in 1977	1977 in 1977
	web builders				
Theridion petraeum[a]		*T. neomexicanum*	1.35	1.41	1.44[b]
	ambushers				
Xysticus montanensis[a]		*Misumenops celer*	1.22[b,c]	1.00	1.00[b]
	jumpers				
Pellenes hirsutus[a]		*Sassacus papenhoei*	1.81	1.18	1.51
	pursuers				
Thanatus foricinus[a]		*Oxyopes scalaris*	1.25[b]	1.00[b]	1.32

[a] Juveniles emerging first in both 1976 and 1977 as measured both by extreme earliest capture and completion of the capturing of the first quartile collected each field season.

[b] At least one of the regressions employed in these comparisons did not have a slope significantly different from zero at the 95% confidence level.

[c] This cohort of *X. montanensis* had a lower body length than *M. celer* during this field season.

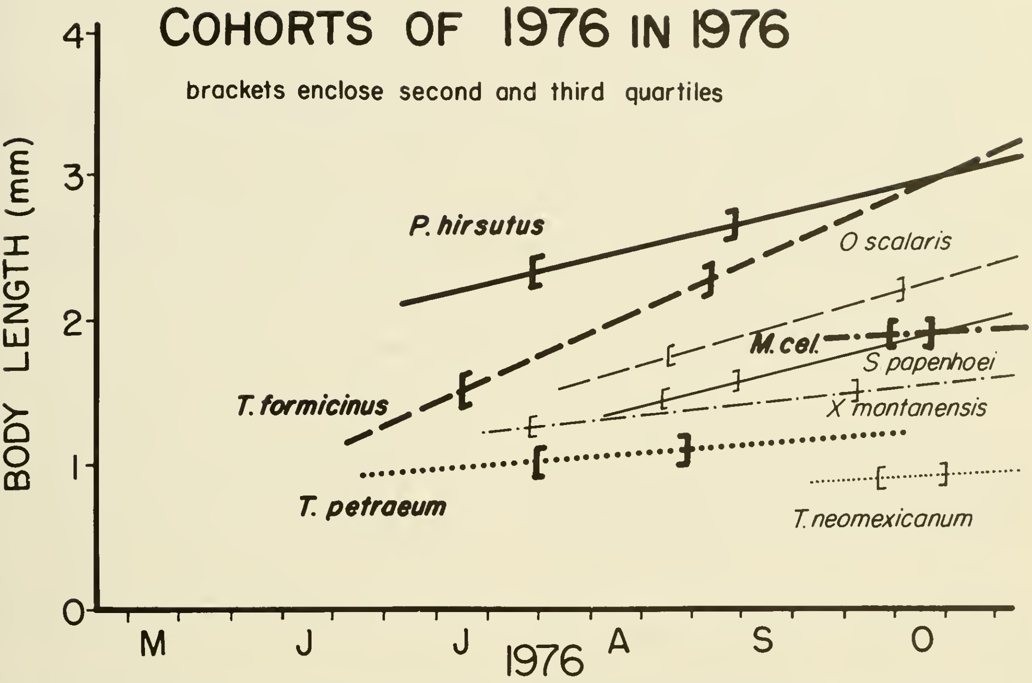

Fig. 7. Body length regression lines for the 1977 cohorts of the eight most abundant spider species collected during the 1977 field season. Hunting strategies are represented by line types described in Figure 5.

their comments and assistance during various stages of this research. This study was aided immeasurably by reference collections developed by Barbara Abraham and Cynthia Hatley and identified by Willis Gertsch. I am particularly grateful to my major professor, James MacMahon, for all he has done for me. This research constitutes part of a dissertation presented to Utah State University.

LITERATURE CITED

BALOGH, J., AND J. LOSKA. 1948. Quantitative-biosoziologische Untersuchung der Arthropodenwelt. Ungarischer Sandgebiete. Arch. Biol. Hung. 18:65–100.

DROOZ, A. T. 1965. Elm spanworm head capsule widths and instars. J. Econ. Entomol. 58:629–631.

DUFFEY, E. 1962. A population of spiders in limestone grassland. J. Anim. Ecol. 31:571–599.

ENDERS, F. 1974. Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other means of coexistence. Ecology 55:317–328.

______. 1975. The influence of hunting manner on prey size, particularly in spiders with long attack distances (Araneidae, Linyphiidae and Salticidae). Amer. Nat. 109:737–763.

______. 1976. Size, food-finding, and Dyar's Constant. Env. Ent. 5:1–10.

GERTSCH, W. J. 1949. American spiders. D. Van Nostrand Co., Princeton, 285 p.

GREENQUIST, E. A., AND J. S. ROVNER. 1976. Lycosid spiders on artificial foliage: stratum choice, orientation preference, and prey wrapping. Psyche 83:196–209.

HATLEY, C. L., AND J. A. MACMAHON. 1980. Spider community organization: Seasonal variation and the role of vegetation architecture. Env. Ent. 9:632–639.

HUTCHINSON, G. E. 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? Amer. Nat. 93:145–159.

JACKSON, R. R. 1977. Prey of the jumping spider *Phidippus johnsoni* (Araneae: Salticidae). J. Arachnol. 5:145–149.

JUDD, W. W. 1965. Studies of the Byron Bog in southwestern Ontario XVIII. Distribution of harvestmen and spiders in the bog. Nat. Mus. Can. Natur. Hist. Pap. 28:1–12.

KASTON, B. J. 1948. Spiders of Connecticut. Hartford: State of Connecticut Bull. 70.

MAY, R. M. 1973. Stability and complexity in model ecosystems. Princeton Univ. Press, Princeton, New Jersey. 235 pp.

MAY, R. M., AND R. H. MACARTHUR. 1972. Niche overlap as a function of environmental variability. Proc. Nat. Acad. Sci. USA 69:1109–1113.

PECK, W. B., AND W. H. WHITCOMB. 1978. Phenology and populations of ground surface, cursorial spiders in a forest and a pasture in south central United States. Symp. Zool. Soc. London 42:131–138.

Riechert, S. E. 1974. Thoughts on the ecological significance of spiders. BioScience 24:352–356.

Robinson, J. V. 1981. The effect of architectural variation in habitat on a spider community: an experimental field study. Ecology 62:73–80.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. MacMillan, New York. 634 pp.

Savory, T. H. 1928. The biology of spiders. Sedgwick and Jackson, London. 376 pp.

Schoener, T. W. 1970. Size patterns in West Indian *Anolis* lizards. II. Correlations with the sizes of particular sympatric species—displacement and convergence. Amer. Nat. 104:155–174.

Tretzel, E. 1955. Intragenerische Isolation und interspezifische Konkurrenz bei Spinnen. Z. Morphol. Okol Tiere 44:43–162.

Turnbull, A. L. 1960. The spider population of a stand of oak (*Quercus robur* L.) in Wytham Wood, Berks., England. Canadian Entomol. 92:110–124.

______. 1973. The ecology of the true spiders (Araneomorphae). Ann. Rev. Ent. 18:305–348.

Uetz, G. W. 1975. Temporal and spatial variation in species diversity of wandering spiders (Aranea) in deciduous forest litter. Env. Ent. 4:719–724.

______. 1977. Coexistence in a guild of wandering spiders. J. Anim. Ecol. 46:531–541.

REPTILES AND AMPHIBIANS OF IDAHO, NO. 2

Wilmer W. Tanner[1]

Abstract.— For about 20 years Richard P. Erwin collected amphibians and reptiles in southwestern Idaho. This report is an attempt to indicate some of his herpetological activities, and to list the numerous individuals, universities, and museums that were recipients of his collections.

In 1941 *The Reptiles and Amphibians of Idaho No. 1* was published (Tanner, 1941, Great Basin Nat. 2:87) as a checklist with a list of the locality records known at that time for each species. Since then, other authors (Brodie 1968, 1970, Teberg 1963) have contributed to the herpetological fauna of the state so that the present report is not presented to add to the known fauna, or to serve in any way as a checklist, but to add additional historical information concerning the state of Idaho.

In 1956, while investigating the distribution and systematics of the Western Skink (*Eumeces skiltonianus*), I had the opportunity to visit with Mr. Harold M. Tucker and Professor O. H. Smith at the College of Idaho in Caldwell. My concern was to discover, if possible, any additional material that might be helpful to a better understanding of these lizards in the western United States. During this visit, I was fortunate in receiving from Mr. Tucker the field books of Mr. Richard P. Erwin, who was perhaps the first authentic collector of herpetological specimens for the state of Idaho; at least his field books, as will be shown, indicate the large number of specimens that were collected and distributed to the museums and researchers throughout the United States.

Although most of his field activities centered around the Boise area, they did include most of the adjoining counties and were particularly associated with the areas near the Snake River to the south and west of Boise. Although Mr. Erwin was a herpetological collector, this was a hobby. Mr. Erwin was an accomplished musician and music teacher, and had his private studio at 19–20 Gem Building, 20th and Main Streets, Boise, Idaho. The correspondence included in the field notes indicates that his home was at 2320 Woodlawn Avenue.

He was born on 28 March 1875 in Indianola, Iowa, and passed away on 4 May 1932 in Boise, Idaho. Although he was a professional musician, much of his free time (according to his field books) was spent investigating the natural history of southwestern Idaho. He was not only concerned with herpetology and entomology, but was also interested in archaeology, with a special interest in Indian rock writing in southwestern Idaho.

The significance of the field notes was that Mr. Erwin provided considerable material that was undoubtedly used not only to augment the collections of many museums and universities, but also for a better understanding of the distribution of western amphibian and reptile species. To indicate the extent of his activities, it is necessary to list the individuals and/or institutions who, according to his field notes, received collections. It appears from his records that one of his most important museums was the Idaho State Historical Museum, in which he established a collection of the amphibians and reptiles of Idaho as he understood them. To accomplish this, he corresponded with professional herpetologists at the various museums where he secured identifications, and also received, on exchange, specimens from other areas in the United States.

Two of his publications appeared in the *Bulletin of the Idaho State Historical Society*, the first coauthored with Mr. Reginald Barker (an entomologist) and the second written by himself. The latter was a descriptive distribution checklist published in 1928. His handwritten manuscript of it is included in one of the field books.

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[1] Life Science Museum, Brigham Young University, Provo, Utah 84602.

The following list of individuals and museums indicates the extent of his effort in securing and exchanging specimens:

Number sent	Date sent	To whom or where sent
17	11 August 1917	Slevin (California Academy)
468	30 September 1917	California Academy of Sciences
15	31 August 1919	Slevin
31	December 1919	Helen T. Gaige, University of Michigan
262	21 November 1921	Slevin at California Academy of Sciences
14	21 November 1921	Slevin
19	11 September 1922	Stejneger, U.S. National Museum
39	11 September 1922	Slevin at California Academy of Sciences
44	11 January 1923	Helen T. Gaige
100	16 September 1923	American Museum in New York
10	25 October 1923	G. K. Noble at American Museum
5	29 October 1923	G. K. Noble at American Museum
29	4 February 1924	Slevin
31	4 February 1924	Henshaw at Museum of Comparative Zoology
57	28 June 1924	Helen T. Gaige
18	13 October 1924	G. K. Noble
13	17 October 1924	Slevin
46	21 October 1924	Karl P. Schmidt at Field Museum in Chicago
60	22 October 1924	Museum of Comparative Zoology in Boston
35	16 December 1924	Field Museum
4	20 June 1925	R. V. Chamberlain, Museum of Comparative Zoology in Cambridge, Massachusetts
150	15 February to 22 May 1926	Idaho State Historical Museum
6	8 March 1926	Slevin
7	19 April 1926	Ortenberger
33	19 April 1926	Fowler
7	15 August to 17 October 1926	G. K. Noble
47	4 October 1926	Slevin
1	27 October 1926	G. K. Noble
33	22 November 1926	Grinnell at the University of California–Berkeley
36	22 November 1926	Brimley
77	9 December 1926	Grinnell
8	9 May 1927	A. I. Ortenberger
21	28 November 1927	Netting at Carnegie Museum in Pittsburgh, Pennsylvania
85	5 March 1928	Netting at Carnegie Museum in Pittsburgh, Pennsylvania
135	11 April 1928	V. M. Tanner in Provo, Utah
1	17 April 1928	Helen T. Gaige
9	23 April 1928	L. M. Klauber in San Diego, California
4	12 June 1928	L. M. Klauber
50	5 July 1928	L. M. Klauber
22	25 February 1929	Field Museum
16	28 April 1929	E. H. Taylor in Lawrence, Kansas
218	16 December 1929	Helen T. Gaige, University of Michigan, Ann Arbor, Michigan
108	1 December 1931	Ralph D. Chamberlain in Salt Lake City, Utah
7	18 December 1931	Dr. Thomas Barbour at the Museum of Comparative Zoology
6	28 June 1932	U.S. National Museum in Washington, D.C.

Of those collections noted in his field books (and there may have been others not recorded), a total of 2,404 specimens were sent to other institutions. The California Academy of Science (J. R. Slevin, recipient) received nearly 40 percent of the material.

I am indebted to the late Mr. Tucker at the College of Idaho in Caldwell, Idaho, and to the Idaho State Historical Society for their generous help in providing some of the information included in this report.

The Erwin field journals are deposited in the Idaho State Historical Society Museum.

NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART X

Stephen L. Woodl[1]

Abstract.— The following species are named as new to science from Mexico: *Corthylus exiguus, lustratus, micacirrus, Dendrocranulus sobrinus, Dendroterus fossifrons, modicus, Gnathotrichus alniphagus, Hylocurus dissimilis, micaceus, scitulus, secus, Phloeoterus burserae, Pseudothysanoes mandibularis, simplex, squameus, truncatus.* The genus *Phloeoterus*, with *P. burserae* as the type-species, is also named as new.

Sixteen species and one genus of Scolytidae are described as new to science from Mexico on the following pages. They represent the genera *Corthylus* (3), *Dendrocranulus* (1), *Dendroterus* (2), *Gnathotrichus* (1), *Hylocurus* (4), *Phloeoterus* (1), and *Psuedothysanoes* (4). The new genus, *Phloeoterus*, is very closely related to *Dendroterus* (Pityophthorina, Corthylini). The discovery of *Gnathotrichus alniphagus* in *Alnus* in Mexico is of particular interest, because of its close relationship to *G. retusus* (LeConte) and the fact that one of the hosts of *G. retusus* is *Alnus*.

Corthylus exiguus, n. sp.

This species apparently represents a new species group that is somewhat intermediate between *collaris* Blandford and *villifer* Wood. It has the declivity much as in *collaris* except that interstriae 3 bears small tubercles. The female frons is more nearly like that of *villifer*, but differs as described below.

Female.— Length 1.0 mm (paratypes 0.8–1.0 mm), 2.3 times as long as wide; color brown, except basal half of pronotoum light brown.

Frons rather strongly concave on a subcircular area from eye to eye from epistoma to well above upper level of eyes, upper margin obtusely rounded; surface smooth, shining, almost impunctate in central area, sparse, moderately coarse punctures in upper and lower areas; vestiture sparse, fine, short. Antennal club with shape similar to *collaris*, suture 1 narrowly grooved and septate on mesal third, 2 aseptate, obscurely, incompletely grooved on mesal half.

Pronotum about as in *collaris*.

Elytra outline similar to *collaris* except much more broadly rounded behind; disc subreticulate, almost subrugose, punctures obsolete except near suture; declivity much steeper, interstriae 1 moderately, narrowly elevated into a carina of uniform height from base to near apex, 2 rather strongly impressed, almost flat, impunctate, shining (punctures on striae 1 and 2 fine, impressed), 3 almost as high as 1, broadly rounded, with punctures replaced by minute granules. Vestiture of a few hairlike setae on declivital interstriae.

Male.— Similar to female except frons planoconvex, reticulate, almost impunctate; antennal club smaller, more nearly symmetrical; anterior margin of pronotum with a pair of moderately large serrations.

Type locality.— Cuautenango, Guerrero, Mexico.

Type material.— The female holotype, male allotype, and six paratypes were taken at the type locality on 23–II–1982, 1650 m, S-573, A. Burjos.

The holotype, allotype, and paratypes are in my collection.

Corthylus lustratus, n. sp.

This species is distinguished from *luridus* Blandford by the less densely pubescent, partly glabrous female frons and by the smaller tubercles on the declivity.

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[1] Life Science Museum and Department of Zoology, Brigham Young University, Provo, Utah 84602. Scolytidae contribution No. 77.

Female.— Length 2.2 mm (paratypes 2.2–2.3 mm), 2.3 times as long as wide; color very dark brown.

Frons similar to *luridus* except median third of lower half of frons glabrous, setae in remaining area shorter, less abundant.

Pronotum and elytral disc as in *luridus;* elytral declivity more evenly convex on upper half, tubercles smaller on all interstriae except 1; declivital setae apparently less numerous, shorter.

Type locality.— "Texecal," Maiote Poztlan, Morelos, Mexico.

Type material.— The female holotype and five female paratypes were taken at the type locality on 1-XI-1982, 1740 m, B-087, A. Burjos.

The holotype and paratypes are in my collection.

Corthylus micacirrus, n. sp.

This species keys to *rubricollis* Blandford in my monograph, but its small size and coloration cause greater confusion with *collaris* Blandford. From *collaris* it is distinguished by the very different female frons, by the larger elytral punctures, and by the total absence of granules on declivital interstriae 1 and 3.

Female.— Length 2.2 mm, 2.4 times as long as wide; color dark brown, basal half of pronotum lighter brown.

Frons much broader, concavity slightly deeper and extending much higher on vertex; vestiture half as long, finer, much more dense. Antennal club more narrowly rounded at apex, cirrus less than half as long, not attaining middle of apical margin.

Pronotum about as in *collaris.*

Elytra similar to *collaris* except punctures rather coarse (three or more times larger), declivity steeper, declivital striae 3 without any indication of granules, striae 1 and 2 with punctures more strongly impressed, vestiture shorter, less numerous.

Type locality.— Chilapa, Guerrero, Mexico.

Type material.— The female holotype was taken at the type locality on 23-II-1982, 1690 m, S-345, *Ardisia* sp., T. H. Atkinson and A. Equihua.

The holotype is in my collection.

Dendrocranulus sobrinus, n. sp.

This species is distinguished from *confinis* Wood by the somewhat less strongly impressed male frons, with the median elevation on the vertex lower, by the more coarsely punctured pronotal disc, with accompanying elevations about a third as large, and by the more broadly, more strongly impressed male declivity.

Male.— Length 2.0 mm (paratypes 1.8–2.1 mm), 2.8 times as long as wide; color dark reddish brown.

Frons as in *confinis* except lower areas less strongly impressed and median elevation on vertex not as high or as sharply defined.

Pronotum as in *confinis* except punctures on posterior half larger (about twice as large near median line), callus (or elevation) accompanying each puncture about a third as large.

Elytra about as in *confinis* except discal punctures smaller (particularly those of interstriae); declivity more strongly, more broadly impressed to striae 3 (transversely, feebly concave).

Female.— Similar to female *confinis* except frons and pronotum less distinctly reticulate, declivity more strongly, broadly flattened.

Type locality.— Veracruz, Veracruz, Mexico.

Type material.— The male holotype, female allotype, and six paratypes were taken on 2-IV-1982, 8 m, *Luffa acutangula*, J. F. Duran. Three specimens not included in the type series, apparently of this species, were taken at Km 56 carr. Xochimilco-Oaxtepec, Morelos, Mexico, 22-I-1980, Cucurbitaceae, T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Dendroterus fossifrons, n. sp.

This species is distinguished from *striatus* (LeConte) by the much larger, deeper excavation on the male frons, by the more scabrous pronotal disc, and by the much coarser elytral vestiture.

Male.— Length 2.0 mm (paratypes 1.8–2.0 mm), 2.5 times as long as wide; color reddish brown.

Frons resembling *striatus* except median third on central (longitudinal) fourth abruptly, deeply excavated.

Pronotum as in *striatus* except posterior areas with more reticulation, granules slightly larger, more numerous.

Elytra as in *striatus* except usually a bit stouter, interstrial punctures usually larger; declivity steeper on lower half, more broadly convex, and with striae 1 and 2 more distinctly impressed, interstrial setae much stouter but not longer.

Female.— Similar to male except frons with a transverse carina as in female *striatus*.

Type locality.— Estación de Biologia, Jalisco, Mexico.

Type material.— The male holotype, female allotype, and 10 paratypes were taken at the type locality on 2–III–1982, 80 m, S–351B, A. Equihua.

The holotype, allotype, and paratypes are in my collection.

Dendroterus modicus, n. sp.

This species is distinguished from *mexicanus* Blandford by the larger size, by the presence of coarse granules on the pronotal disc, by the steeper elytral declivity, and by other characters cited below.

Female.— Length 2.4 mm, 2.4 times as long as wide; color reddish brown.

Frons about as in *mexicanus*, with episomal calluses equal to less than average size for that species.

Pronotum 1.08 times as long as wide; resembling *mexicanus* except anterior margin more broadly rounded and disc armed by subcrenulate tubercles as in *sallaei* Blandford.

Elytra 1.4 times as long as wide; similar to *mexicanus* except strial punctures on disc much deeper, interstrial punctures closer, declivity much steeper, with interstriae 2 more distinctly impressed and lateral summits more pronounced.

Type locality.— Volcan Ceboruco, Nayarit, Mexico.

Type material.— The female holotype was taken at the type locality on 5–VII–1965, 1100 m, *Bursera*, S. L. Wood.

The holotype is in my collection.

Gnathotrichus alniphagus, n. sp.

This species is distinguished from *retusus* (LeConte) by the more strongly, much more extensive aciculation of the frons, by the finer pronotal and elytral punctures, and by the less strongly impressed declivital sulcus. The discovery of this species in *Alnus* greatly magnifies interest in the fact that the closely related *retusus* also has *Alnus* as one of its hosts.

Female.— Length 3.6 mm (paratypes 3.6–3.7 mm), 3.5 times as long as wide; color very dark brown (holotype almost black).

Frons resembling *retusus* except with rather coarse convergent aciculation on more than median two-thirds almost to upper level of eyes; antennal club a bit larger, with sutures more distinctly arcuate.

Pronotum as in *retusus* except punctures on posterior areas slightly smaller, not as close.

Elytra resembling *retusus* except strial punctures smaller, impressed points smaller, less numerous, impressed transverse lines longer, much more abundant; declivity not as steep, sulcus much less strongly impressed, tubercles on lateral summits smaller.

Type locality.— Fierro del Toro in southwest Morelos, Mexico.

Type material.— The female holotype and four female paratypes were taken at the type locality on 30–VII–1982, 2650 m, B–026, *Alnus firmifolia*, A. Burjos and E. Saucedo.

The holotype and paratypes are in my collection.

Hylocurus dissimilis, n. sp.

This species is distinguished from *incomptus* Wood by the smaller, stouter average size, by the much more conspicuous, much coarser elytral setae, and by details of the declivity described below.

Male.— Length 2.0 mm (paratypes 1.8–2.0 mm), 2.4 times as long as wide; color almost black, vestiture pale.

Frons and pronotum essentially as in *incomptus* except setae on pronotal disc much coarser.

Elytra 1.4 times as long as wide; about as in *incomptus* except interstrial granules near base of declivity and on face of declivity smaller, lower half of declivity less strongly impressed, all denticles smaller; interstrial setae from base to apex of stout bristles (almost scalelike, about 10 times as long as wide), longest near base of declivity (each as long as distance between rows), distinctly shorter near base, shorter and more slender on lower declivity.

FEMALE.— Similar to male except transverse frontal carina not as sharp or as high; interstrial setae longer, more slender, pointed (but much coarser than in *incomptus*).

TYPE LOCALITY.— Estación de Biología, Chamela, Jalisco, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and eight paratypes were taken at the type locality on 4–III–1982, 70 m, S–368, Sapindaceae, A. Equihua.

The holotype, allotype, and paratypes are in my collection.

Hylocurus micaceus, n. sp.

This species is distinguished from *dissimilis* Wood by the smaller size and reddish brown color, by the finer sculpture, and by details of the elytral vestiture and declivity as described below.

MALE.— Length 1.3 mm (paratypes 1.3–1.4 mm), 2.5 times as long as wide; color reddish brown.

Frons similar to *dissimilis* except transverse carina slightly shorter, not as high, surface more finely reticulate.

Pronotum about as in *dissimilis* except more finely sculptured, posterior areas more finely reticulate, tubercles smaller.

Elytra 1.6 times as long as wide; similar to *dissimilis* except strial punctures smaller, interstriae smoother, shining, upper declivity more strongly convex, declivital granules and tubercles slightly larger, apical portion of interstriae 9 more strongly elevated, almost carinate toward apex of elevated area. Vestiture largely restricted to declivity; erect interstrial scales almost as long as distance between rows, blunt, each about eight times as long as wide, scales shorter and sparse on lower declivity.

FEMALE.— Similar to male except transverse frontal carina weak to obscure.

TYPE LOCALITY.— Estación de Biología, Chamela, Jalisco, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and four paratypes were taken on 20–VIII–1982, 100 m, S–764, A. Equihua.

The holotype, allotype, and paratypes are in my collection.

Hylocurus scitulus, n. sp.

This species is distinguished from *elegans* Eichhoff by the much steeper male elytral declivity, with many other differences in declivital sculpture, and by the more evenly convex female frons, with the patch of setae on the vertex undivided.

MALE.— Length 1.2 mm (paratypes 2.1–2.4 mm), 2.7 times as long as wide; color dark brown, vestiture pale.

Frons and pronotum essentially as in *elegans* except pronotal disc less clearly reticulate.

Elytral disc similar to *elegans* except striae more strongly impressed near base of declivity, strial punctures slightly smaller; declivity much steeper than in *elegans*, terminal mucro longer, more acutely pointed, spines in circumdeclivital row much larger, each (1–8) projecting caudad a distance equal to its basal width, strial punctures near margins much larger. Vestiture about as in *elegans* except scalelike setae at margin of declivity forming a row around apex of each circumdeclivital spine (transverse direction) (in *elegans* these scales remain in uniseriate, longitudinal arrangement).

FEMALE.— Similar to female *elegans* except frons more evenly convex, patch of setae on upper area not divided on median line; declivital setae longer, coarser, lower area less broadly impressed.

TYPE LOCALITY.— Estación de Biología, Chamela, Jalisco, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and six paratypes were taken at the type locality on 2–VII–1982, 50 m, S–748, *Acacia*, A. Equihua.

The holotype, allotype, and paratypes are in my collection.

Hylocurus secus, n. sp.

This species represents a new species group. It is distinguished from all other members of the genus by the strongly procurved sutures of the antennal club, by the male circumdeclivital row of tubercles in which tubercle 8 is carinate and almost joins 9, which continues on a declining course to the apex, and by the unique declivity.

Male.— Length 2.2 mm (paratypes 2.0–2.2 mm), 3.6 times as long as wide; color reddish brown.

Frons moderately, transversely impressed at level of antennal insertion, convex above; convex surface rugose-reticulate; a few stout setae almost scalelike.

Pronotum almost as in *aberrans* Wood except disc reticulate and partly rugose anteriorly, with fine, shallow punctures rather numerous, most punctures with a fine granule on their posterior margin.

Elytra 1.6 times as long as wide; sides straight and subparallel on basal four-fifths, very slightly wider at base of declivity; striae not impressed except at base of declivity, punctures rather large, deep, smaller on basal fourth; interstriae slightly narrower than striae, almost smooth, punctures small, shallow, uniseriate; base of declivity abrupt, armed by a circumdeclivital row of tubercles, tubercles rather large, feebly or not projecting behind. Declivity subtruncate, abrupt, very steep, face convex, summit on interstriae 1 below middle; strial punctures in rows on basal half, largely confused below; interstriae somewhat shagreened, without punctures; 1 normal on basal third and apical fifth, greatly widened (about three times) at and below middle and strongly elevated to two summits, upper summit submammiform, lower summit subacutely pointed. Glabrous, except a few very minute strial setae on lower declivity; interstrial scales on disc abraded.

Female.— Similar to male except frons a bit more irregularly convex, punctures more evident, ornamented by rather abundant, coarse, moderately long setae, particularly on upper half; declivity rounded, without circumdeclivital row of tubercles; declivital sculpture about as on disc except interstrial punctures replaced by fine, rounded granules; elytral vestiture consisting of minute strial hair and rows of erect interstrial scales, each scale about as long as distance between rows, widest on distal half, about six times as long as wide.

Type locality.— Estación de Biología, Chamela, Jalisco, Mexico.

Type material.— The male holotype, female allotype, and four paratypes were taken at the type locality on 3-III-1981, 100 m, S-359, Leguminosae, A. Equihua.

The holotype, allotype, and paratypes are in my collection.

Phloeoterus, n. gen.

This is the fourth genus to be placed in the *Dendroterus* genus group. It is distinguished from *Dendroterus* Blandford by the 5-segmented antennal funicle and by the unique sculpture of the female head.

Description.— Male frons essentially convex, female impressed, armed by tubercles, and ornamented by setae; eye emarginate; antenna as in *Dendroterus* except funicle 5-segmented; pronotum with basal and lateral margins rounded; elytra and tibiae about as in *Dendroterus*.

Type-species.— *Phloeoterus burserae* Wood, described below.

Phloeoterus burserae, n. sp.

This species resembles a few *Dendroterus* species, but it is distinguished by the generic characters, most particularly by the unique female frons.

Female.— Length 1.7 mm (paratypes 1.6–1.8 mm), 2.7 times as long as wide; color yellowish brown, anterior slope of pronotum and elytral declivity much darker.

Frons shallowly, broadly concave from epistoma to upper level of eyes, armed on median fourth slightly above upper level of eyes by an acute, transverse carina and by a pair of rather coarse tubercles near lateral margin just above level of antennal insertion; surface smooth, shining, punctures minute, rather sparse, almost uniformly distributed; vestiture sparse and rather short on concave area, much longer and more abundant on upper and lateral margins.

Pronotum as in *Dendroterus eximius* Wood except reticulation and punctures much finer.

Elytra as in *D. eximius* except strial punctures more sharply impressed on disc, punctures becoming obsolete on declivity, elytral vestiture similar but only half as long.

Male.— Similar to female except male frons resembling male *D. eximius* (weakly convex, unarmed by tubercles or carina, without conspicuous setae).

Type locality.— Estación de Biología, Jalisco, Mexico.

Type material.— The female holotype, male allotype, and 10 paratypes were taken at the type locality on 2–II–83, 100 m, S-865, *Bursera instabilis*, T. H. Atkinson and N. Bautista M.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes mandibularis, n. sp.

This species apparently represents a species group previously unreported. The male resembles the female of the *dislocatus* (Blackman) group of species except that the mandibles are elongate (similar to *Gnatholeptus shannoni* Blackman) and the frons is convex.

Male.— Length 1.1 mm (paratype 1.1 mm), 2.7 times as long as wide; color yellowish brown.

Frons convex above, becoming flattened toward epistoma; surface almost smooth, subreticulate, without evident punctures; vestiture sparse, short, inconspicuous. Mandibles elongate, meeting on median line, resembling those of *Gnatholeptus shannoni*.

Pronotum similar to *dislocatus* except anterior margin and anterior slope more broadly rounded.

Elytra similar to *dislocatus* except anterior margin and anterior slope more broadly rounded.

Elytra similar to *dislocatus* except declivity shorter, steeper; interstrial punctures replaced by small, rounded granules on disc and declivity; strial setae more consistently present and slightly longer; on declivity interstrial scales decreasing in width and length toward apex to about half that of setae at base of declivity.

Type locality.— Estación de Biología, Chamela, Jalisco, Mexico.

Type material.— The male holotype and one male paratype were taken at the type locality on 2–VII–1982, 130 m, ultraviolet light, A. Equihua.

The holotype and allotype are in my collection.

Psuedothysanoes simplex, n. sp.

This species belongs to the *phoradendri* Blackman species group and is placed near *furvescens* Wood. From *furvescens* it is distinguished by the smaller average size, by the minute, almost obsolete strial punctures on disc and declivity, and by the minute but conspicuous strial hair.

Male.— Length 1.1 mm (paratypes 1.1–1.3 mm), 2.4 times as long as wide; color very dark brown, summit of pronotum usually reddish brown, vestiture pale.

Frons similar to *furvescens* except lower half a bit more extensively flattened, central fovea more conspicuous.

Pronotum as in *furvescens* except anterior margin much more broadly rounded, discal and lateral areas smoother, sparse punctures minute.

Elytra more slender than in *furvescens*, with declivity steeper, restricted to shorter area; striae not indicated, punctures almost obsolete, minute punctures each bearing a minute hairlike seta; interstriae indicated by obscure, setiferous, minute punctures; surface almost smooth, shining. Declivity restricted to posterior third, steep, convex; sculpture as on disc except interstrial punctures replaced by minute granules. Vestiture consisting of minute strial hair, and erect interstrial scales; each scale about four times as long as wide, spaced between rows and between scales within a row by slightly more than length of a scale.

Female.— Similar to male except body a bit more slender and elytral interstrial scales slightly longer and up to six times as long as wide.

Type locality.— Estación de Biología, Chamela, Jalisco, Mexico.

Type material.— The male holotype, female allotype, and six paratypes were taken at the type locality on 2–II–1983, 30 m, S-856, T. H. Atkinson and N. Bautista.

The holotype, allotype, and paratypes are in my collection.

Psuedothysanoes squameus, n. sp.

This species represents a species group previously unknown in North America. The near absence of sutures in the antennal club, stout body, and unusual elytral scales, particularly in the male, distinguish it from other known species.

Male.— Length 1.2 mm (paratypes 1.1–1.5 mm), 2.2 times as long as wide; color rather light reddish brown, elytra usually darker.

Frons rather strongly, transversely impressed on lower two-thirds of area below upper level of eyes, strongly convex above; surface granulate above, finely subgranular in impressed area. Antennal club moderately large, oval, without sutures except 1 obscure, 1 and 2 indistinctly marked by setae.

Pronotum about as in *truncatus* Wood.

Elytra 1.4 times as long as wide, 1.5 times as long as pronotum; striae weakly impressed at base of declivity, punctures moderately coarse, deep; interstriae slightly wider than striae, apparently smooth, shining, punctures small, close, unseriate. Declivity steep, convex, occupying slightly more than posterior third; sculpture much as on disc except strial punctures somewhat smaller; striae end before apex. Vestiture of rows of erect interstrial scales, those on disc short, each about twice as long as wide, distinctly longer and as wide as an interstriae at base of declivity (each at least as wide as long), very closely spaced, decreasing in length toward apex until less than one-third that of longest scales.

Female.— Similar to male except frons concavely excavated on more than median three-fourths from epistoma to slightly above eyes, upper margin of concavity acutely carinate; strial punctures much smaller, not as deep, interstrial punctures obscure; vestiture of elytral disc continued on declivity, without any enlarged scales; elytral declivity not as steep or as broad.

Type locality.— Estación de Biología, Chamela, Jalisco, Mexico.

Type material.— The male holotype, female allotype, and eight paratypes were taken on 27–V–1982, 50 m, S–485, *Lonchocarpus*, T. H. Atkinson and A. Equihua.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes truncatus, n. sp.

This species belongs to the *heliura* Wood species group, but it is unique in having the declivital strial punctures in rows and no interstrial punctures or armature.

Male.— Length 1.6 mm, 2.1 times as long as wide; color yellowish (anterior) to reddish brown (posterior areas).

Frons as in *heliura* except conspicuous setae broadly scalelike in central and upper areas.

Pronotum about as in *heliura* except summit wider.

Elytra 1.2 times as long as wide, stouter than in *heliura* with declivity much steeper, more abruptly truncate, declivital face less strongly convex; disc with striae not impressed, punctures rather coarse, deep; interstriae smooth, shining, only slightly wider than striae, punctures uniseriate, small becoming replaced by small granules on basal half. Declivity abruptly truncate, not quite vertical; circumdeclivital costa complete, subacute, its summit not smooth, obscurely subserrate; declivital face distinctly, rather broadly impressed near margins, moderately convex on lower half, with an indefinite summit on interstriae 3 just below middle; striae not impressed, punctures in rows, punctures rather coarse at base, gradually decreasing in size, rather small toward apex; interstriae smooth, shining, impunctate (except 3 punctured) 2 gradually constricted until obsolete on lower fourth, 3 expanding slightly in width just below middle, with a row of punctures. Vestiture consisting of rows of short interstrial scales on disc, each about two to four times as long as wide; circumdeclivital costa bearing a row of rather large scales, each about two to four times as long as wide; declivital interstriae 3 bearing a row of long erect scales, each three times as long as those in circumdeclivital row and eight or more times as long as wide, a few similar scales on 5.

Type locality.— Playa Perula, Jalisco, Mexico.

Type material.— The male holotype was taken on 3–III–1982, 10 m, S–356, *Randia* sp. (Rubiaceae), A. Equihua.

The holotype is in my collection.

NEW RECORDS OF DIATOMS FROM BLUE LAKE WARM SPRING, TOOELE COUNTY, UTAH

Samuel R. Rushforth[1] and Irena Kaczmarska[1],[2]

Abstract.— Blue Lake Warm Spring in Tooele County, Utah, contains a rich diatom flora with a significant number of taxa that are unusual in this region. We have identified a total of 136 taxa in our samples from this locality, several of which are new records for Utah and North America.

Our studies of Blue Lake Warm Spring were initiated as a part of larger studies on the algal floras of spring systems of the Great Basin, including projects on warm springs (St. Clair and Rushforth 1976), cool seeps (St. Clair and Rushforth 1978), and wet wall hanging gardens (Rushforth et al. 1976, Clark and Rushforth in press, Johansen, Rushforth, and Brotherson 1983, Johansen et al. 1983). This investigation has provided valuable information on diatom floristics, ecology, and distribution. The present paper presents data on those species that we have determined to be new records for North America and/or Utah.

Site Description

Blue Lake Warm Spring is near the border of Nevada and Utah in Tooele County, Utah. This spring system consists of many small springs and two major pools. The larger is about 20 m deep, and the smaller about 3 m deep. They are interconnected by streams and are surrounded by several acres of wet marsh.

Blue Lake waters are mesothermic, with a temperature range between 25 and 29 C. These waters can be classified as mesohaline brackish, with total dissolved solids measured at 4831 mg/l. The most common ions were sodium and chloride. Sulfates were also somewhat elevated at 219 mg/l.

Methods

A total of 27 samples was obtained over a nine-year period from various depths and localities at the Blue Lake site. The first 16 samples were obtained in March 1973 by taking sampling vials to various depths of the larger pool, using scuba gear. Periphyton and sediment samples were collected in February 1977 from under the ice of the smaller pool. The last 9 samples were collected from the smaller pool in July 1982. They were obtained from the edge and bottom of the pool by diving.

Permanent diatom slides were prepared following standard methods with boiling nitric acid cleaning procedures (St. Clair and Rushforth 1976).

Results and Discussion

A total of 136 species was collected and identified during this study. They are described, more thoroughly discussed, and illustrated in a companion paper (Kaczmarska and Rushforth 1983). The species that represent new records for North America and for Utah are noted in Table 1 and illustrated in Figures 1–39.

Several of the species we encountered in Blue Lake Warm Spring were unusual and difficult to place into known taxa. Some species of *Achnanthes*, *Navicula*, *Nitzschia*, and others were only tentatively placed into previously described species. In such cases, for the present paper, the distribution is given for the taxa of tentative placement of our specimens.

Our Blue Lake flora was very different from typical diatom floras of the standing

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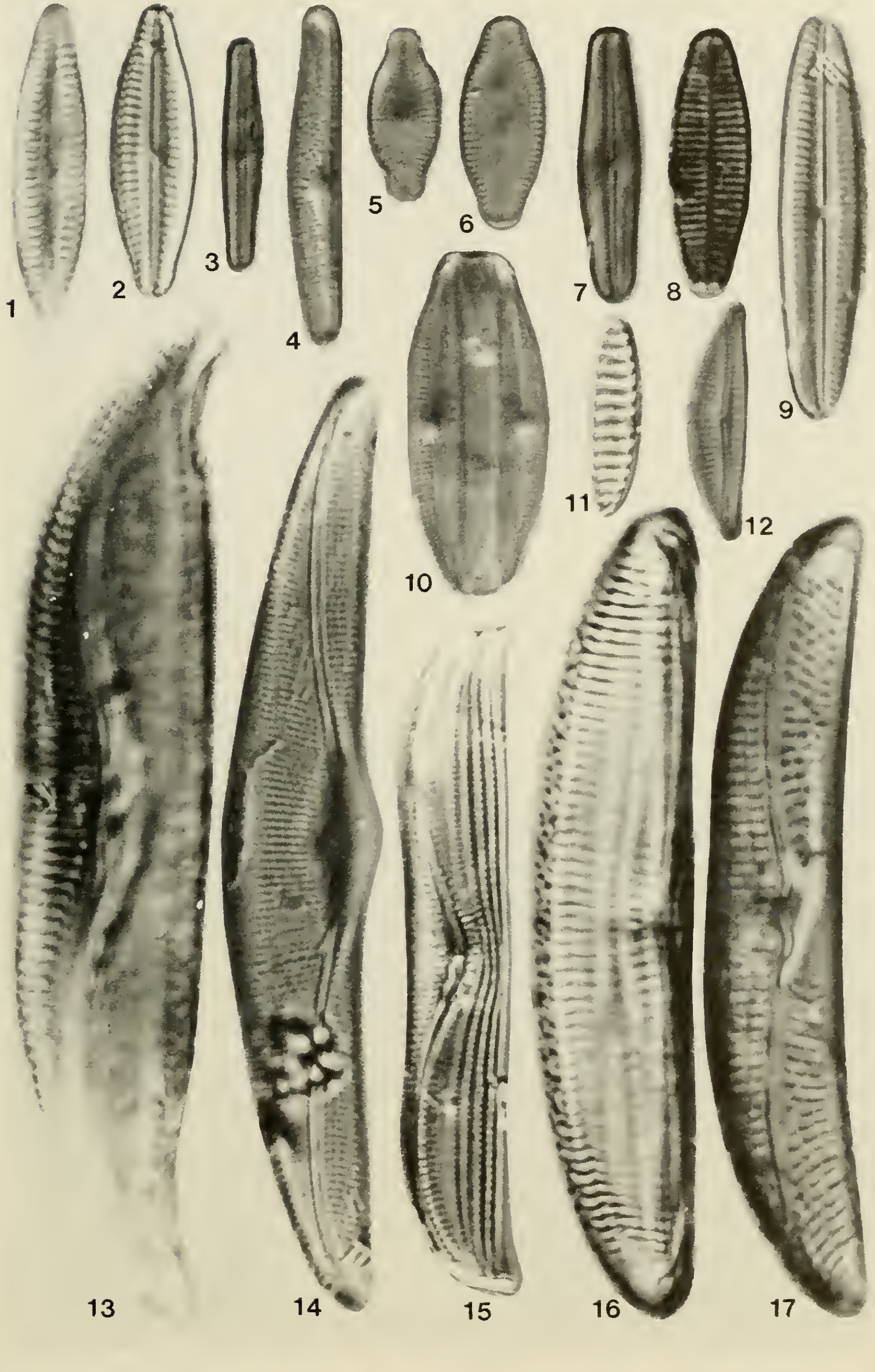
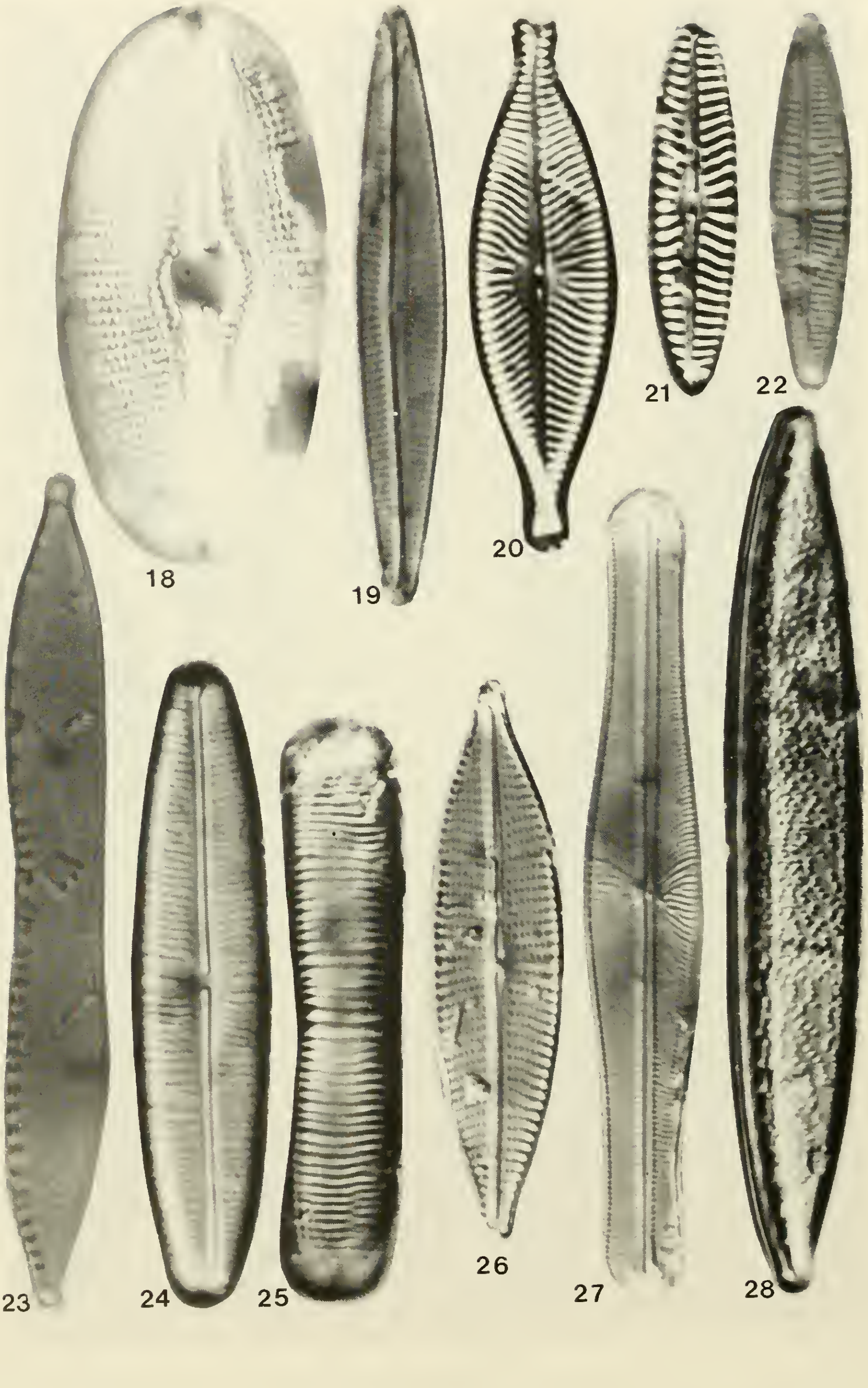
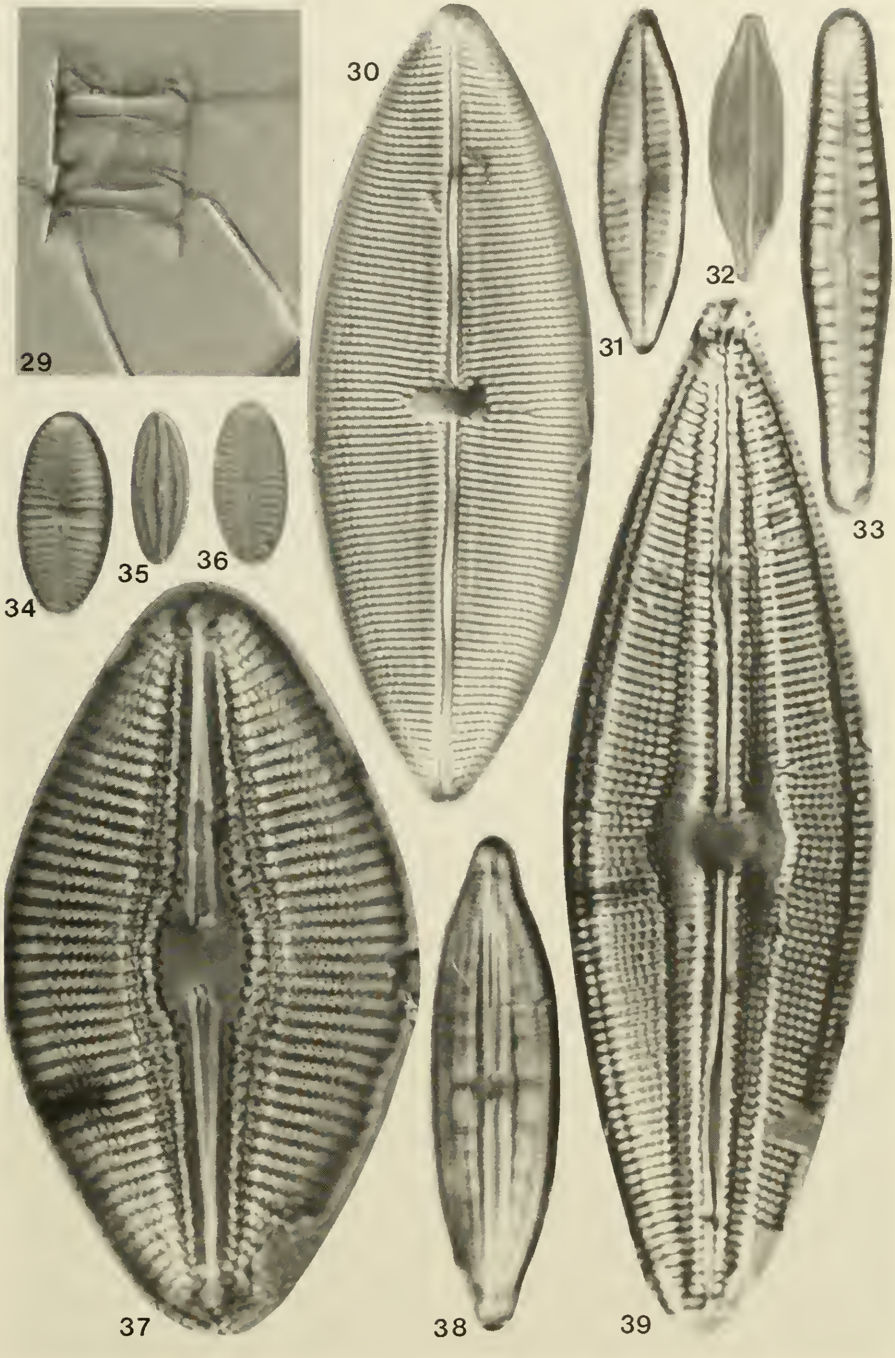


Figs. 1–17: 1, *Achnanthes similis* rapheless valve; 2, *Achnanthes similis* raphe valve; 3, *Achnanthes* cf *atomus* var. *congolensis* raphe valve; 4, *Anomoeoneis follis*; 5, *Achnanthes* cf *submarina* raphe valve; 6, *Achnanthes* cf *submarina* rapheless valve; 7, *Achnanthes tropica* raphe valve; 8, *Achnanthes* cf *subhudsonis* rapheless valve; 9, *Achnanthes cottoriensis* raphe valve; 10, *Amphora coffeaeformis* var. *perpusilla*; 11, *Denticula* cf *parva*; 12, *Cymbella fonticola*; 13, *Amphora commutata*; 14–15, *Amphora arcus* var. *sulcata*; 16, *Amphora proteus*; 17, *Amphora proteus* var. *oculata*. All figures are X2200.



Figs. 18–28: 18, *Diploneis subovalis*; 19, *Navicula feuerborni*; 20, *Navicula salinarum* var. *capitata*; 21, *Navicula digitoradiata*; 22, *Stauroneis legleri*; 23, *Nitzschia pseudostagnorum*; 24, *Navicula subinflatoides*; 25, *Navicula subinflatoides* girdle view; 26, *Navicula zanoni*; 27, *Navicula pseudocrassirostris*; 28, *Nitzschia vitrea* cf var. *scaphiformis*. All figures are X2200.



Figs. 29–39: 29, *Chaetoceros amanita* girdle view of short chain X1095; 30, *Mastogloia aquilegiae*; 31, *Navicula cryptocephaloides*; 32, *Navicula longirostris*; 33, *Gomphonema intricatum* cf var. *fossilis*; 34, *Navicula parva*; 35, *Navicula subsulcatoides*; 36, *Navicula submuralis*; 37, *Diploneis smithii* f. *rhombica*; 38, *Mastogloia pumila*; 39, *Mastogloia brauni*. All figures are X2200 except where noted.

Table 1. Alphabetical listing of diatom species identified in our samples collected from Blue Lake Warm Spring that represent new records for North America and/or for Utah. Those species new from North America are labeled NA, and those previously collected in North America but new for Utah are labeled U.

Achnanthes cf *atomus* Hust. var. *congolensis* Hust.	NA
Achnanthes cotteriensis Foged	NA
Achnanthes similis Hust.	NA
Achnanthes cf *subhudsonis* Hust.	U
Achnanthes tropica Hust.	NA
Achnanthes cf *submarina* Hust.	U
Amphora arcus Greg. var. *sulcata* (A.Sm.) Cl.	U
Amphora coffeaeformis Ag. var. *fossilis* Pant.	NA
Amphora coffeaeformis var. *perpusilla* Grun.	U
Amphora commutata Grun.	U
Amphora macilenta Greg.	NA
Amphora proteus Greg.	U
Amphora proteus var. *oculata* Perag.	NA
Amphora tenuissima Hust.	U
Anomoeoneis follis (Ehr.) Cl.	U
Chaetoceros amanita A. Cl.	NA
Cymbella fonticola Hust.	NA
Diploneis smithii (Breb.) Cl. f. *rhombica* Meresch.	U
Diploneis subovalis Cl.	U
Fragilaria construens var. *subsalina* Hust.	U
Fragilaria lapponica var. *minuta* Cl.	U
Gomphonema intricatum cf var. *fossilis* Pant.	NA
Mastogloia aquilegiae Grun.	NA
Mastogloia brauni Grun.	U
Mastogloia pumila (Grun.) Cl.	U
Navicula cryptocephaloides Hust.	NA
Navicula digitoradiata (Greg.) A. Sm.	U
Navicula feuerborni Hust.	NA
Navicula longirostris Hust.	U
Navicula muralis Grun.	U
Navicula parva (Menegh.) Cl.	NA
Navicula pseudocrassirostris Hust.	NA
Navicula subinflatoides Hust.	U
Navicula subsulcatoides Hust.	NA
Navicula submuralis Hust.	U
Navicula zanoni Hust.	U
Nitzschia pseudostagnorum Hust.	NA
Nitzschia vitrea Norm. cf var. *scaphiformis* Wisl. & Poretz.	U
Pinnularia brebissonii (Kuetz.) Cl. var. *diminuta* Grun.	U
Stauroneis legleri Hust.	U
Terpsinoe intermedia Grun.	U

waters of our region. It was also unexpectedly different from the floras of other studied thermal systems in North America. This is particularly evident from Table 1, where it may be seen that 41 of our taxa represent new records from North America and/or Utah, which represents 31% of the total flora. Because of the unusual nature of the Blue Lake flora, we are continuing our studies of thermal systems in the Great Basin of North America. We hope to provide information on diatom floristics and ecology, particularly on the chemical and physical factors important in shaping diatom communities.

Literature Cited

Clark, R. L., and S. R. Rushforth. In press. A study of the algal flora of selected hanging gardens of Glen Canyon, Utah. Great Basin Nat. Mem.

Johansen, J. R., S. R. Rushforth, and J. D. Brotherson. 1983. The algal flora of Navajo National Monument, Arizona, USA. Nova Hedwigia 38:501–553.

Johansen, J., S. R. Rushforth, R. Orbendorfer, N. Fungladda, and J. A. Grimes. 1983. The algal flora of selected wet walls in Zion National Park, Utah, USA. Nova Hedwigia 38:765–808.

Kaczmarska, I., and S. R. Rushforth. 1983. The diatom flora of Blue Lake, Tooele County, Utah. Bibliotheca Diatomologica 2(1):1–123

Rushforth, S. R., L. L. St. Clair, A. T. Leslie, H. K. Thorne, and D. C. Anderson. 1976. The algal flora of two hanging gardens in southeastern Utah. Nova Hedwigia 27:231–323.

St. Clair, L. L., and S. R. Rushforth. 1976. The diatom flora of the Goshen Warm Spring ponds and wet meadows, Goshen, Utah, USA. Nova Hedwigia 28:353–425.

______. 1978. The diatom flora of the Goshen Playa and wet meadow. Nova Hedwigia 29:191–229.

HOST TISSUE RESPONSE FOR TROUT INFECTED WITH *DIPHYLLOBOTHRIUM CORDICEPS* LARVAE

Terry N. Otto[1] and Richard A. Heckmann[1]

Abstract.— *Diphyllobothrium cordiceps* (Leidy 1871) plerocercoids are present as enzootic parasites in the viscera and skeletal muscle of cutthroat trout (*Salmo clarki*) from Yellowstone National Park, Wyoming. Eight cutthroat trout from the Yellowstone River were examined by histological technique and scanning electron microscopy to determine the response of host tissue to the presence of diphyllobothriid larvae. All fish sampled contained encysted plerocercoids on the serosa of the pyloric caeca and intestine. In addition to infection of the exterior of the alimentary tract, muscle tissue was infected in two of the fish sampled, whereas one fish had infection of the liver, spleen, and testis. Intact plerocercoids were encapsulated with connective tissue that was infiltrated with lymphocytes and macrophages. Granulomatous tissue that was fibrotic was also present. Pancreatic tissue was displaced in infections associated with the alimentary tract. The liver showed general necrosis with edema, and the spleen demonstrated a reduction in cellularity and increased connective tissue. Testicular tissue compressed by an adjacent plerocercoid appeared to be in an otherwise normal stage of development. Necrotic myofibrils near encapsulated parasites were separated by edema and fatty infiltration. A brief morphologic description of *D. cordiceps* is presented. In general, *D. cordiceps* did not appear to produce a serious debilitation of cutthroat trout.

The plerocercoids in the life cycle of *Diphyllobothrium cordiceps* are enzootic in salmonids of Yellowstone National Park (YNP) and lakes of the Northern Rockies. This parasite, found primarily in cutthroat trout (*Salmo clarki*), has been reported in rainbow trout, brook trout, brown trout, and grayling (Post 1971). After the initial discovery by Hayden (1872), the diphyllobothriid plerocercoids of YNP began to receive a great amount of attention and study. The history of *D. cordiceps* epitomizes the taxonomic confusion that is prevalent for the plerocercoid (metacestode) stage of *Diphyllobothrium*.

Presence of diphyllobothriid larvae in trout of Yellowstone Lake was first recorded during Hayden's 1872 scientific exploration of Yellowstone Park (Hayden 1872). Plerocercoids were sent to Leidy, who referred the forms to *Dibothrium cordiceps* (=*Diphyllobothrium cordiceps*). Leidy's determination of *Diphyllobothrium* larvae present in Yellowstone trout was later verified by Linton (1891a, 1891b). Due to a high incidence of infection, public and scientific interest persists concerning *D. cordiceps* in trout of Yellowstone Park (Post 1971). The aesthetic appearance of infected fish has been of major concern to YNP biologists. Currently the number of plerocercoid infected trout that have been discarded by fishermen in YNP is estimated to be approximately 300 fish per month (Varley 1978).

Concerning the cestode from infected YNP fish, Skinker (1933) made a comparative study and reported that *D. cordiceps* and *D. latum* were synonomous. Since *D. latum* was known to be pathogenic for man (Davis 1953), more definitive research was necessary. To determine whether a public health danger was present, Woodbury (1935) ingested in two trials plerocercoids from Yellowstone trout. He concluded that humans were unsuitable hosts when no viable eggs of helminth parasites were found after administering an anthelminthic to himself. Meyer and Robinson (1963) evaluated Scott's (1955) redescription of *D. cordiceps* as inadequate for comparative studies, and then stated that *D. sebago* resembled *D. cordiceps*.

Confusion concerning the taxonomic status of *D. cordiceps* and other members of the genus still exists. The problem was appropriately summarized by Stunkard (1965), who quoted a colleague as saying, "The problem is one that might lead a respectable taxonomist to give up and to go into molecular biology."

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The life cycle of *D. cordiceps* for YNP is similar to other *Diphyllobothrium* species. The definitive hosts were listed by Scott (1935) as White Pelican (*Pelicanus erythrorhyncus*), California Gull (*Larus argentatus*), and American Merganser (*Mergus merganser americanus*). Eggs are passed from the definitive host's feces into the water, where they hatch into coracidia. First intermediate host crustaceans ingest the coracidia. The crustacean host has not been identified and was once thought to be *Diaptomus* (Post 1971). Recent work implicates *Eucyclops agilis* (Kingston et al. 1980) as a first intermediate host, but the results are under scrutiny. The infected crustaceans are eaten by fish, the second intermediate host, which passes the developed plerocercoid to piscivorous birds.

Histopathogenesis has not been described for *D. cordiceps* larvae in cutthroat trout of YNP. However, there are pathological descriptions of other diphyllobothriid plerocercoids in trout. For example, *Diphyllobothrium sebago* does not encyst but penetrates the heart and liver in brook trout, causing extensive hemorrhage (Hoffman and Dunbar 1961). *Diphyllobothrium dendriticum* produces edematous granulation tissue in the body cavity with a severe anemia (Hickey and Harris 1947).

The two objectives of this work are to assess the tissue damage in YNP cutthroat trout by *D. cordiceps* plerocercoids and to provide a brief morphological description of *D. cordiceps* larvae at the light and electron microscope levels.

Materials and Methods

In May 1979, four cutthroat (*Salmo clarki*) were taken by line from each of two locations, Fishing Bridge and Le Hardy Rapids, on Yellowstone River, which drains from Yellowstone Lake, Yellowstone National Park, Wyoming. Plerocercoids (metacestodes) were excised from muscle and viscera and fixed in 10% neutral buffered formalin for light microscopy. Glutaraldehyde was used to fix plerocercoids for scanning electron microscopial (SEM) studies of the larvae.

Approximately 50 tissue samples were processed according to standard methods (Humason 1972) for light microscopy (LM). The samples were embedded in Paraplast, sectioned at 6 μm, and stained using Harris hematoxylin (H & E), Giemsa (G), and Mallory's trichrome (MT). Periodic-acid Schiff reaction (PAS) was used to demonstrate mucopolysaccharides (Galigher and Kozloff 1971, Humanson 1972). Cytological and histological structures of trout tissue, as outlined by Anderson (1974), were observed and pathological changes recorded. The morphometric data for *D. cordiceps* were recorded from sections of plerocercoids in five observations of 10 different sections.

Sections of host tissue containing cestode larvae were fixed with 3% buffered glutaraldehyde followed by standard dehydration methods. The samples were mounted on a specimen holder, coated with gold in a CS minicoater sputter apparatus, and viewed with an AM Ray 1000 A high resolution SEM operating at 10 kv. Micrographs were taken at varying magnifications. Permanent data on the micrographs are registered with a digital data keyboard entry system attached to the AM Ray SEM. On each micrograph the KV, magnification, micron bar, plate number, laboratory location, and specimen code (PLER CES) are printed at the bottom.

Results and Discussion

Cysts were found in all cutthroat trout sampled. The majority of the cysts were attached to the alimentary tract (Fig. 1). However, 3 fish had infections of other organs.

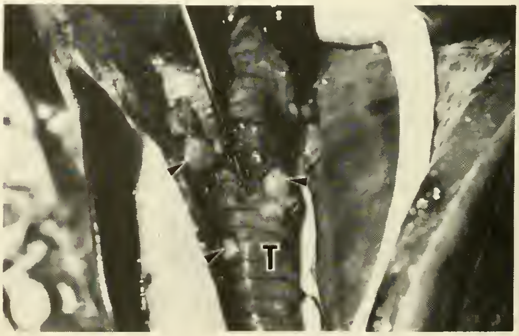

Fig. 1. Encysted plerocercoids of *Diphyllobothrium cordiceps* (arrows) along intestinal tract (T).

Both liver and spleen in one fish were infected with diphyllobothriid plerocercoids, and another individual trout had a plerocercoid infection of the testis and muscle adjacent to the kidney. In a third instance a single plerocercoid was observed encysted in the hypaxial muscle. Cysts varied from white to light brown and were approximately 2 mm in diameter and 1–2 mm thick. Cysts were either in intimate contact or were attached to the serosa of the alimentary tract by a pedunculated string of connective tissue (CT). The plerocercoid infection of the testis was a peritoneal attachment, and those of the muscle, liver, and spleen were next to the parenchyma. Examination of cysts using histologic technique showed some cysts to contain larvae, whereas other cysts appeared to have degenerating parasites, presumably *D. cordiceps*, with granulomatous tissue present.

The reaction of cutthroat trout to infection with *D. cordiceps* was a multicellular connective tissue chronic inflammatory response. Plerocercoids were encapsulated by dense CT (Figs. 2 and 3) and infiltrated predominantly by lymphoid cells with occasional macrophages. For some plerocercoid infections a short acute phase characterized by congestion, edema, and hemorrhage is usually followed by the longer lasting chronic phase typified by CT encapsulation (Cosgrove 1975).

A characteristic granulomatous inflammatory response was present around apparent degenerative parasites with lymphocytes, macrophages, and epitheloid cells as demonstrated by G and MT stains. PAS positive cells were usually found in the interior milieu and may be cells of the mononuclear phagocyte system.

Chronic inflammation leading to fibrosis is characteristic in many diseases of fish and results in the encystment of a parasite as a method of isolating an irritating agent (Cosgrove 1975, Hauck 1977, Heckmann and Jensen 1978). Many of the sections that were prepared had a pronounced affinity for aniline blue of MT, which indicates an active fibrosis in capsules surrounding *D. cordiceps* (Arme and Owen 1967, 1969).

Encapsulation of a parasite removes it from many of the host defense mechanisms, thus reducing parasitic stress to some degree. Attempts by the host to remove or resolve the parasitic infection may continue within the capsule.

In long-term infections fibrous capsules can become calcified, resulting in death of the plerocercoid (Sweeting 1977). No evidence of calcification was observed in this sample or in previous research on *D. cordiceps* by other authors.

Intestine and pyloric ceca adjacent to the cyst had an edematous muscularis externa, and degenerative adipose, displacement of pancreatic tissue, and occasional mononuclear infiltration of the muscularis mucosa and externa (Fig. 2). Fibrosis of adipose and pancreatic tissue appeared to be more extensive near cysts with degenerating parasites than those with intact larvae.

There seemed to be no reaction in the intestinal mucosa related to the presence of cestode larvae on the serosal surface, which might interfere with digestion. In one instance there was hyperplastic CT around a submucosal cyst that extended into the intestinal lumen. The cause of the cyst was not apparent. The cyst was also accompanied by a disruption of the stratum compactum and inner circular muscle layer of the muscularis externa. The injury to the mucosa was localized and minor.

Only one instance of gonadal infection was observed in a male cutthroat trout. The CT of the tunica albuginea was hyperplastic in close proximity to the cestode larva. The capsule was typically infiltrated with lymphocytes and macrophages. A major effect

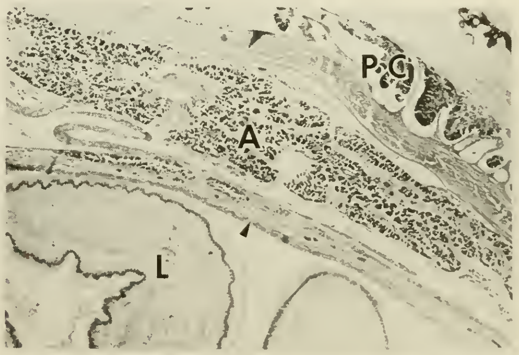

Fig. 2. Fibrosis of adispose and pancreatic tissue (A) with edema of pyloric ceca (PC) near *Diphyllobothrium cordiceps* larva (L) in connective tissue capsule (arrow). H & E X 25.

was the compression of the seminiferous tubules (Fig. 4). In spite of the compression, germinal tissue in the seminiferous tubules appeared to be in a normal stage of development as compared to Henderson's (1962) description of brook trout testis. Gonadal retardation in fish has been caused by other pseudophyllidean larva (*Ligula intestinalis*), which produced an atrophic condition where it was difficult to separate reproductive tissue from mesenteries (Arme 1968). Since Woodbury (1935) stated that sterility of trout could result from a *D. cordiceps* infection, a more thorough investigation of gonadal infection rate and possible effects on germinal tissue and gonadotropic hormones should be pursued.

Skeletal muscle was not extensively infected in this sample, as only two of eight fish had noticeable encysted larvae. Effects of plerocercoid larvae in muscle produced degeneration and necrosis of nearby myofibrils, fatty infiltration, and edema. Mononuclear infiltration of the adipose and CT was concomitant. In one fish, larvae encysted near kidney tissue produced an edematous condition, interruption of the epithelial limiting membrane, and hypertrophy of the renal organ. Cells of the kidney appeared to be in a normal condition. The necrosis present in muscle sections studied would probably not produce a serious debilitation of the trout.

A single infection of liver by a *Diphyllobothrium* plerocercoid induced necrosis of hepatocytes (Fig. 5). Melanomacrophages, lymphocytes, and tissue macrophages were present, indicating active phagocytosis of dead host tissue and parasite by-products. Connective tissue infiltration, localized fibrosis, into the sinusoids was also prevalent. The plerocercoid was intact and did not appear degenerative.

Hepatocyte necrosis is not common in many parasite infections (Cosgrove 1945), but in severe infections general necrosis may occur (Hauck 1977) with extensive damage (Stromberg and Crites 1974). As long as the infection persists, fibrous scarring and cirrhosis might result in reduced liver function. Obstruction and portal hypertension may occur when sinusoids are compressed or occluded (Stromberg and Crites 1974).

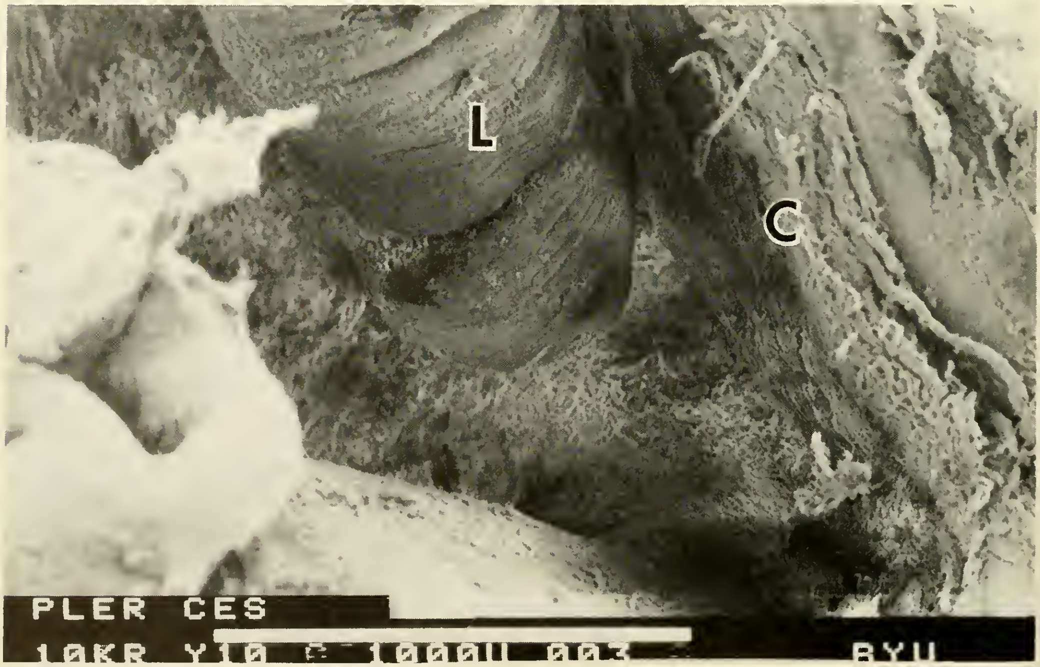

Fig. 3. Plerocercoid of *Diphyllobothrium cordiceps* (L) partially removed from connective tissue capsule (C).

One instance of spleen infection by plerocercoid larvae produced a compression of the spleen but no necrosis. The spleen appeared edematous, with a decrease in germinal center size and cellularity and an increase of CT in the stroma. There was an abundance of melano-macrophages distributed fairly evenly throughout the spleen. Erythropoiesis is an important function of the spleen (Lane 1979). Therefore, damage to the spleen, whether partial or total, could lead to anemia and accompanying reduced vigor. Depending upon the incidence of spleen infection in the cutthroat trout of YNP, damage to the erythropoietic centers in the spleen may be an important factor contributing to any observed ill-health of infected fish (Ellis 1979).

The histopathogenesis of *D. cordiceps* larvae in YNP cutthroat trout did not appear to be gravely debilitating. The chronic inflammation associated with *D. cordiceps* plerocercoids is typical of such a parasitic infection. The amount of damage to infected viscera was minimal except perhaps in the case of spleen and liver, both of which had structural changes that could be detrimental to the health of the trout. The infection appears to be long term, and a decrease in vigor of infected fish may result from the presence of large numbers of *D. cordiceps* larvae.

Little attention has been given to numbers of *D. cordiceps* larvae in cutthroat trout. Scott (1935) recorded approximate plerocercoid populations ranging from 50 or more in each fish. Heckmann (1971) observed over 400 plercercoid larvae in one cutthroat trout. Extensive studies have not been recorded elucidating effects of sublethal infections of *D. cordiceps* larvae on the health of cutthroat trout, either. Histologic examination of *D. cordiceps* in the viscera and muscle did not appear to cause lesions that would be damaging to the point of impairment, except in the case of liver and spleen infection.

Woodbury (1935) stated that the physiological well-being of cutthroat trout infected with *D. cordiceps* larvae could be compromised by reduced vitality or sterility. Parasitism by other pseudophyllidean larvae produced poor condition, reduction in size, and anemia in host fish (Arme and Owen 1969, Hickey and Harris 1949, Mahon 1976, Pitt and Grundman 1957). Although not seen in our sampling period, Linton (1891) described heavily infected fish of Yellowstone Lake as being emaciated. He also observed erratic swimming of infected fish, which has also been seen in recent years (Post 1971) in YNP.

The major impact of YNP cutthroat trout infected with *D. cordiceps* seems to be aesthetic. Response of fishermen has been to discard infected trout. In July 1959, 7500 uncleaned trout were found in garbage cans of YNP. This same survey was duplicated in 1978, and a monthly estimate of discarded trout for the month of July was approximately 300 (Varley 1978). A decrease in discarded trout was probably due to a change of legal size limit in which only younger fish were kept. Presumably the younger fish would have a lower worm burden and would be more acceptable to sportsmen (Varley 1980).

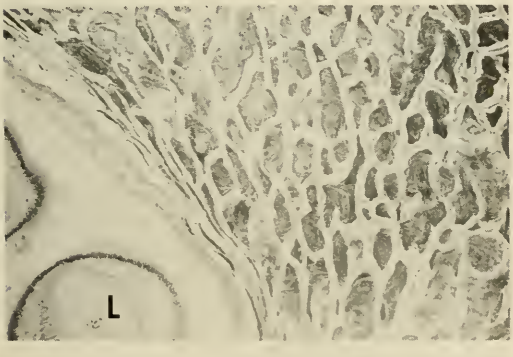

Fig. 4. Compression of testis by encysted *Diphyllobothrium cordiceps* larva with fatty infiltration and edema. H & E X 25.

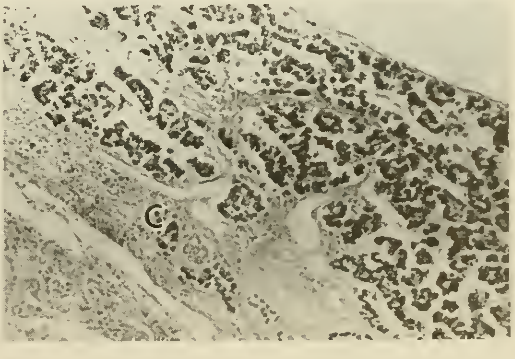

Fig. 5. Necrotic hepatocytes with fibrosis adjacent to capsule (C) of cestode larva. H & E X 25.

The value of histologic features of *Diphyllobothrium* plercercoids for taxonomic purposes was cited by Halvorsen (1970), Kuhlow (1953), and Meyer (1963). Some morphological characteristics often used in the study of diphyllobothriid larvae are length of microtrichia, thickness of the integument, and longitudinal parenchymal musculature. These and other histologic features are shown in Figure 6.

Length and morphology of microtrichia have been used for taxonomic purposes both at the LM (Halvorsen 1970) and SEM (Anderson 1975) levels. The length of microtriches (Table 1) was shorter than some other species of *Diphyllobothrium* (Halvorsen 1970). The measurement of microtriches was hampered since they do not lie flat, nor was the base properly seen in histological sections.

In the SEM microphotographs of the surface topography for *D. cordiceps* larvae, microtrichia appear slender (Fig. 7) and somewhat densely arranged. The scolex region is contracted with bothridia visible as a shallow groove with a decreased number of microtrichia. The integument of *D. cordiceps* larvae had shallow folds. *Diphyllobothrium* integument has active metabolic properties (Arme 1966, Von Bonsdorff et al. 1971), and PAS staining showed presence of mucopolysaccharides in the integument. No PAS reaction was seen in the plerocercoid environment precluding possible alkaline phosphatase activity by *D. cordiceps* larvae (Moog and Wenger 1952). The integument was approximately 8.6 μm thick (Table 1). The longitudinal parenchymal musculature (PM) was approximately 88.1 μm. The longitudinal parenchymal musculature may vary in thickness in various parts of the body of diphyllobothriid plerocercoids (Halvorsen 1970). Therefore, due to the fact that the plerocercoids were sectioned in situ, the morphometric data for the longitudinal parenchymal muscle may require further study on relaxed whole larvae.

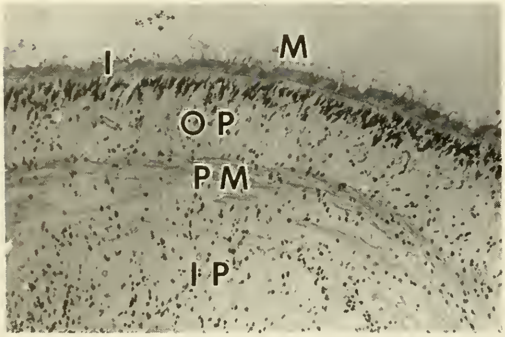

Fig. 6. Longitudinal section of *Diphyllobothrium cordiceps* larva showing some morphological features: microtrichia (M), integument (I), outer parenchyma (OP), longitudinal parenchymal muscle (PM), and inner parenchyma (IP). H & E X 100.

Earlier in the history of *D. cordiceps*, the larvae were believed to be similar to *D. latum* (Skinker 1933). It is evident from the morphometric data supplied by this report that *D. cordiceps* does not resemble *D. latum* since the latter has considerable differences in morphology (Halvorsen 1970). Comparisons of histologic structures of *D. cordiceps* larvae can be made with other *Diphyllobothrium* plerocercoids to assist in establishing the identity of *D. cordiceps* in cutthroat trout of YNP.

Acknowledgments

We thank the National Park Service at Yellowstone National Park for their help on this project and James Allen of the Brigham Young University Electron Optics Laboratory for his help with the scanning electron microscopy.

Literature Cited

Anderson, B. G., and D. L. Mitchum. 1974. Atlas of trout histology. Wyoming Game and Fish Department, Bulletin 13. 110 pp.

Anderson, K. 1975. Comparison of surface topography of three *Diphyllobothrium* (Cestoda, Pseudophyllidea) by scanning electron microscopy. Int. J. Parasit. 5:293–300.

Table 1. Measurements of anatomical features of *Diphyllobothrium cordiceps* larvae. Mean ± S.E. and range are given in μm.

Length of microtrichia	8.2 ± 0.6 (4.0 – 20.0)
Thickness of integument	8.6 ± 0.3 (4.0 – 14.0)
Thickness of longitudinal parenchymal musculature	88.0 ± 11.8 (24.0 – 247.0)
Width of sections	606.9 ± 21.5 (400.0 – 1030.0)

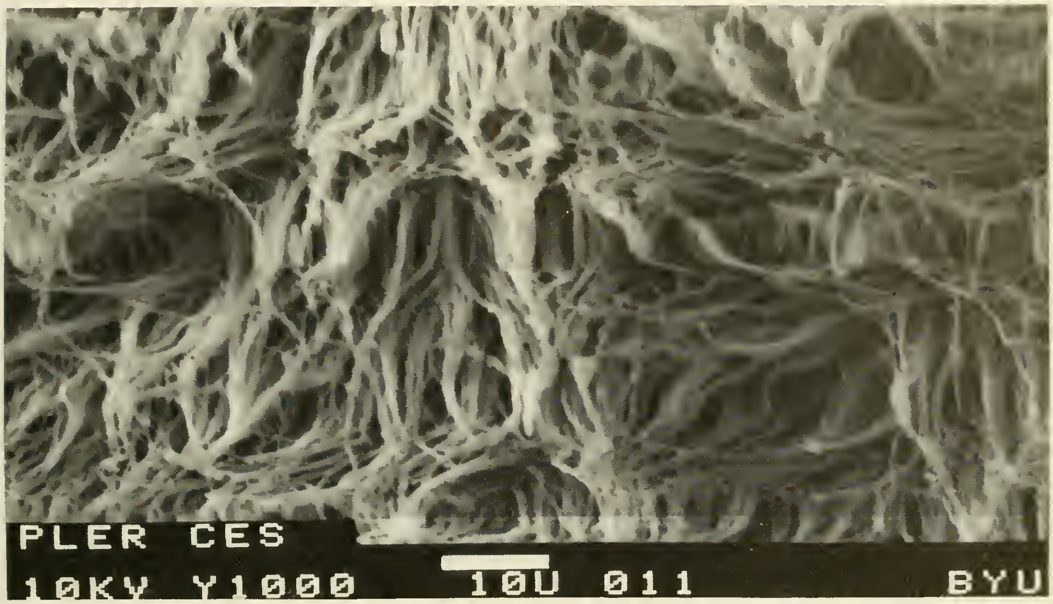

Fig. 7. Microtrichia appear slender and densely arranged.

Arme, C. 1966. Histochemical and biochemical studies on some enzymes of *Ligula intestinalis* (Cestoda: Pseudophyllidea). J. Parasit. 52:63–68.

____. 1968. Effects of the plerocercoid larva of a pseudophyllidean cestode, *Ligula intestinalis*, on the pituitary gland and gonads of its host. Biol. Bull. 134:15–25.

Arme, C., and R. W. Owen. 1967. Infections of the three-spined stickleback, *Gasterosteus aculeatus* L., with the plerocercoid larvae of *Schistocephalus solidus* with special reference to pathological effects. Parasitology 57:301–314.

____. 1969. Observations on a tissue response within the body cavity of fish infected with the plerocercoid larvae of *Ligula intestinalis* (L.) J. Fish Biol. 2:35–37.

Cosgrove, G. E. 1975. Parasites in tissue sections: recognition and reaction. *In* William E. Ribelin and George Migaki, Pathology of fishes. Univ. of Wisconsin Press, Madison, Wisconsin. 1004 pp.

Davis, H. S. 1953. Culture and diseases of game fishes. Univ. of California Press, Berkeley. 322 pp.

Ellis, A. E. 1977. The leucocytes of fish: a review. J. Fish Biol. 11:453–491.

Galigher, A. E., and E. N. Kozloff. 1971. Essentials of practical microtechnique. 2d ed. Lea and Febiger.

Halvorsen, O. 1970. Studies on the helminth fauna of Norway XV: On the taxonomy and biology of plerocercoids of *Diphyllobothrium* Cobbold (1858) from north-western Europe. Nytt Mag. Zool. 18:113–174.

Hauck, A. K. 1977. Histopathologic alterations associated with *Anisakis* larvae in Pacific herring from Oregon. J. Wildl. Dis. 13:290–293.

Hayden, F. V. 1872. The trout of Yellowstone Lake (infected with *Dibothrium cordiceps* Leidy). Pages 97–98 *in* Prelim. Rept. U.S. Geol. Surv. Montana (1871).

Heckmann, R. A. 1971. Parasites of cutthroat trout from Yellowstone Lake, Wyoming. Prog. Fish Cult. 33:103–106.

Heckmann, R. A., and L. Jensen. 1978. The histopathology and prevalence of *Henneguya sebasta* and *Kudoa clupeidae* in the Rockfish, *Sabastes paucispinis* of Southern California. J. Wildl. Dis. 14:259–262.

Henderson, N. 1962. The annual cycle in the testis of the eastern brook trout, *Salvelinus fontinalis*. Canadian J. Zool. 4:631–641.

Hickey, M. D., and J. R. Harris. 1947. Progress of the *diphyllobothrium* epizootic at Poulaphouca Reservoir, Co. Wicklow, Ireland. J. Helminthol. 22:13.

Hoffman, G. L., and C. E. Dunbar. 1961. Mortality of the eastern brook trout caused by plerocercoids (Cestoda: Pseudophyllidea: Diphyllobothridae) in the heart and viscera. J. Parasit. 47:399–400.

Humason, G. L. 1972. Animal tissue techniques. 3d ed. W. H. Freeman and Co., San Francisco. 641 pp.

Kingston, N., K. L. Diem, D. Mitchum, K. K. McKenzie, and S. Hill. 1980. *Diphyllobothrium cordiceps*: A tapeworm problem in Yellowstone Lake fishes. New investigations into the life cycle. 12th annual conference of Rocky Mountain Parasitologists Abstract 15, Univ. of Wyoming, Laramie.

Kuhlow, F. 1953. Bau-und differential diagnose heimischer *diphyllobothrium*—Plerocercoide. Z. Tropen Med. Parasit. 4:186–202.

Lane, H. C. 1979. Some haematological responses of normal and splenectomized rainbow trout (*Salmo gaidneri*) to a 12% blood loss. J. Fish Biol. 14:159–164.

LEIDY, J. 1872. Notice of some worms collected during Professor Hayden's expedition to the Yellowstone River in the summer of 1871. Pages 99–108 *in* Prelim. Rept. U.S. Geol. Surv. Montana.

LINTON, E. 1891a. On two species of larval dibothria from the Yellowstone National Park. Bull. U.S. Fish Comm. 9:64–79.

______. 1891b. A contribution to the life history of *Dibothrium cordiceps* Leidy, a parasite infesting trout in Yellowstone Lake. Bull. U.S. Fish Comm. 9:337–358.

MAHON, R. 1976. Effect of the cestode *Ligula intestinalis* on spottail shiners, *Notropis hudsonius*. Canadian J. Zool. 54:2227–2229.

MEYER, M. C., AND E. S. ROBINSON. 1963. Description and occurrence of *Diphyllobothrium sebago* (Ward, 1910) J. Parasit. 49:969–973.

MOOG, R., AND E. L. WENGER. 1952. The occurrence of a neutral mucopolysaccharide at sites of high alkaline phosphatase activity. Amer. J. Anat. 90:339–372.

PITT, C. E., AND A. W. GRUNDMAN. 1957. A study into the effects of parasitism on the growth of the yellow perch produced by the larvae of *Ligula intestinalis*. Proc. Helm. Soc. Washington 24:73–80.

POST, G. 1971. The *Diphyllobothrium* cestode in Yellowstone Lake, Wyoming. Page 24 *in* Research Journal 41, Agricultural Experiment Station, Univ. of Wyoming, Laramie.

SCOTT, J. W. 1935. On the *Diphyllobothrium* of Yellowstone Park. J. Parasit. 21:443.

______. 1955. A new description of *Diphyllobothrium cordiceps* (Leidy, 1872). Rev. Iber. Parasit., Tomo Extraord., pp. 33, 47–70.

SKINKER, M. D. 1933. Comparative study of *Diphyllobothrium cordiceps* and *D. latum*. J. Parasit. 19:162.

STROMBERG, P. C., AND J. L. CRITES. 1974. Trienophoriasis in Lake Erie white bass *Morone chrysops*. J. Wildl. Dis. 10:352–358.

STUNKARD, H. W. 1965. variation and criteria for generic and specific determinatin of *Diphyllobothrium* cestodes. J. Helminthol. 39:381–296.

SWEETING, R. A. 1977. Studies on *Ligula intestinalis*: Some aspects of the pathology in the second intermediate host. J. Fish Biol. 10:43–50.

VARLEY, J. D. 1978. Garbage can patrol. Page 79 *in* Fishery management program in Yellowstone National Park. Technical Report, U.S. Dept. Int., Fish and Wildlife Service.

______. 1980. Personal communication.

VON BONSDORFF, C.-H., T. FORSTEN, M. D. S. GUSTAFFSON, AND G.-J. WILKGREN. 1971. Cellular composition of plerocercoids of *Diphyllobothrium dendriticum* (Cestoda). Acta. Zool. Fenica 132:1–25.

WOODBURY, L. A. 1935. Infectivity of the plerocercoids of *Diphyllobothrium cordiceps* (Leidy) for man. J. Parasit. 21:315.

ORIENTATION AND SLOPE PREFERENCE IN BARREL CACTUS (*FEROCACTUS ACANTHODES*) AT ITS NORTHERN DISTRIBUTION LIMIT

James Ehleringer[1] and Donna House[1]

Abstract.— Microsite distribution and diurnal tissue temperature fluctuations were measured in *Ferocactus acanthodes* (barrel cactus) at its northern distribution limit in the Beaver Dam Mountains of southwestern Utah. At this location, barrel cacti were limited to south-facing slopes. Orientation (azimuth and angle) of both the cactus stem and of the apical region at the top of the cactus were nonrandom, strongly facing south. The potential adaptive significance of this orientation in minimizing apical meristematic tissue damage under low wintertime conditions and minimizing high temperature damage under summertime conditions is discussed.

Barrel cactus (*Ferocactus acanthodes* (Lemaire) Britt. and Rose) is a globular-columnar cactus common to the warm desert regions of southwestern North America (Shreve and Wiggins 1964, Benson 1982). It is commonly found on rocky, well-drained slopes. Overall, the distribution of this species is from northeastern Baja California in the south to the lower slopes of the Beaver Dam Mountains, Utah, in the north. Little is known about the factors limiting the distribution of this species, although Nobel (1980a) has suggested that *F. viridescens*, a small globular species, is limited to warmer sites than *F. acanthodes* because of its smaller size and greater heat loss characteristics.

Low wintertime temperatures can be an important factor limiting the distributions of many cacti (Shreve 1911, 1914; Turnage and Hinckley 1938). Osmotic water potentials of Sonoran Desert cacti range from –0.4 to –1.8 MPa (Walter and Stadelmann 1974), which will lower the freezing point less than 1 C. Minimum temperatures on the slopes of the Beaver Dam Mountains are often below freezing, and 24-hour periods of subfreezing temperatures are rare, but known to occur (U.S. Weather Bureau Records). Thus, freezing tissue temperatures would appear to be possible at the northern distribution limit of the barrel cactus.

The purpose of this study was to investigate factors influencing the distribution of *F. acanthodes* at its northern distribution limit. To do this, we measured the relationships between plant density and microdistribution as related to wintertime solar radiation heating and the diurnal tissue temperature fluctuations in the winter and summer seasons.

Methods and Materials

The study site was on the southwestern slopes of the Beaver Dam Mountains in an area within 1 km of Castle Cliffs (lat. 37°04′ N, lat. 113°52′ W). The mean elevation of the sites sampled was approximately 1250 m. *Ferocactus acanthodes* (Lemaire) Britt. & Rose was studied in situ on the rocky slopes where they occur in the transition zone between the Great Basin and Mohave Desert vegetation types. This transition community was dominated by *Larrea divaricata*, *Coleogyne ramosissima*, *Krameria parviflora*, *Prunus fasciculata*, *Opuntia acanthocarpa*, and *Yucca brevifolia*.

Cactus tissue temperatures were measured at a depth of 2–3 mm below the epidermal surface using 24-gage copper-constantan thermocouples. Air temperature at 50 cm was measured with a 24-gage copper-constantan thermocouple shielded to reduce radiation errors. All temperature data were sampled at one-minute intervals using a portable micrologger (model CR21, Campbell Scientific, Logan, Utah) and averaged over a 60-minute period.

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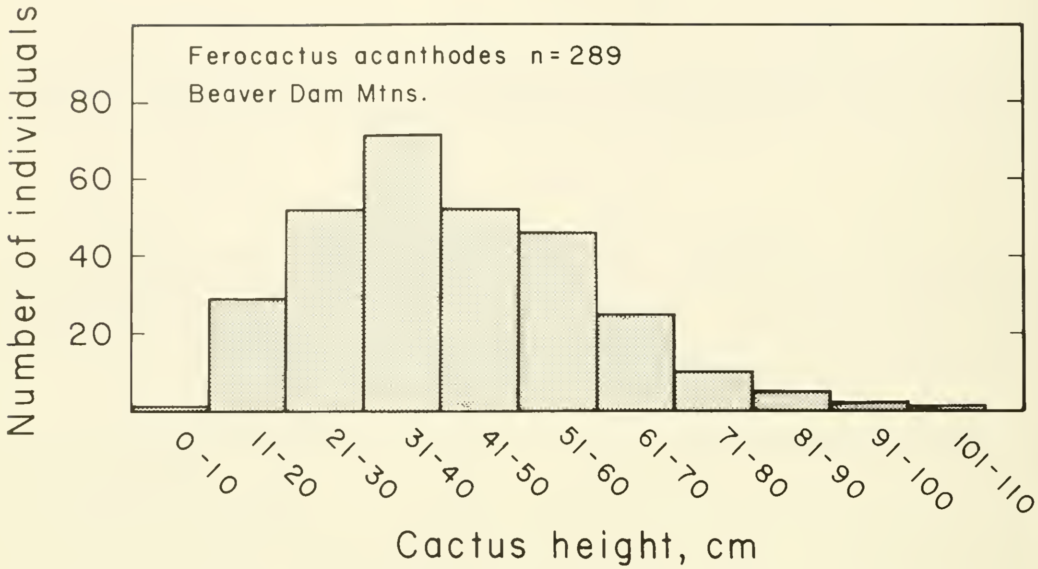

Fig. 1. Frequency histogram for height of *Ferocactus acanthodes* individuals in the Castle Cliffs population in the Beaver Dam Mountains, Utah.

Orientation of the barrel cactus and of the slopes were determined by measuring the azimuth and the inclination. Azimuth was measured with a compass to the nearest 5 degrees and corrected for magnetic deviation from true north. In expressing azimuth data, zero is due south, east is -90°, and west is +90°. Inclination was measured with an inclinometer to the nearest 5 degrees, with a horizontal surface being 0°. Mean azimuths and angular dispersion were calculated trigonometrically as described by Zar (1974). Angular dispersion is used as a measure of the variance about the mean angle. Angular dispersions range from a maximum dispersion of 0 to a minimum dispersion of 1, with maximum dispersion being refined by a perfectly uniform distribution of angles around the circle (and an undefined mean angle) (Zar 1974).

In measuring the orientation of the cactus, two separate sets of measurements were collected. First, the tilt or orientation of the cactus body was measured. Second, the orientation of the apical region at the top of the cactus, which is planar, was also measured.

Calculations of the amount of direct solar radiation incident on a slope were made using equations available in Campbell (1977) and List (1966).

Barrel cactus densities were measured on slopes with different orientations. All slopes within the area were sampled, but data are presented for only those slopes having barrel cacti. For these data, the slope area sampled was determined by the size of the slope that had a uniform orientation and varied in area from 100 m^2 to 2800 m^2.

RESULTS

Barrel cactus height at this site, which is the northern distribution limit for the species was not uniform (Fig. 1). Plant height varied from 10 cm to 107 cm, with the mode being 31-40 cm. There was no difference between the height distributions of barrel cactus with neighboring plants and those without neighboring plants, and therefore the two distributions were lumped. The height distribution was skewed to the left, and only 15% of the plants were taller than 60 cm. For the most part, the smaller plants were globular. The larger the cactus was, the more columnar was its shape. Diameter was only correlated with height for the smaller individuals. In larger cactus, the diameter was essentially constant. As a consequence, 88% of the plants had diameters 20-39 cm.

Orientation of the cactus was determined by measuring the angles and azimuths of the

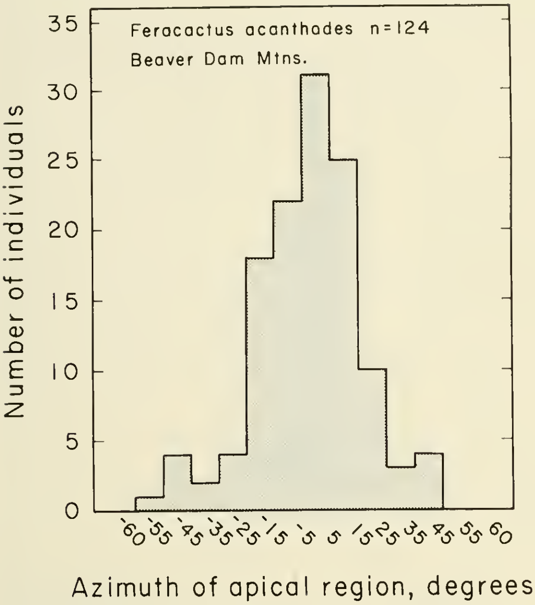

Fig. 2. Frequency histogram for azimuth direction of the apical meristematic region of *Ferocactus acanthodes* in the Castle Cliffs population in the Beaver Dam Mountains, Utah. South is 0°, east is −90°, and west is +90°.

apical region and of the entire body. There was a strong tendency for the apical region of the cactus to face south mean azimuth of 5.7° and a dispersion of 0.88 (Fig. 2). In fact, 77% of the apical regions were facing within 15° of due south. There was also a strong tendency for the body of the cactus to tilt from the vertical. The mean azimuth direction of the tilt was 4.8° with a dispersion of 0.82 (n = 124), which again was in effect facing south. The mean angle of the apical region plant was 33.8° ± 1.3° (Fig. 3). There were 35% of the angles in the 31°–40° range and 76% 21°–50°. Body angles of the entire cactus showed essentially the same variation as the angles of the apical region plane and averaged 47.5° ± 2.3°.

As a consequence of their large mass and nonrandom orientations, cactus tissue temperatures were above air temperatures for much of the time, and the diurnal variation in tissue temperatures was orientation specific. Figure 4 shows the diurnal course of air and tissue temperatures in the winter and summer seasons. Although cactus tissue temperatures were correlated with air temperatures, there was a time lag for this response and the response was very much dependent on a consideration of azimuth orientation. Tissue temperatures on the east side of the cactus warmed quickly after sunrise, peaking before noon and slowly declining throughout the remainder of the day. Tissue temperatures on the west side of the cactus exhibited an almost opposite response, with temperatures peaking in the late afternoon (data not presented). Tissue temperatures on the apical region and the south-facing cactus tissues tracked air temperature changes during the summer, but greatly exceeded air temperatures during the winter, when the solar elevation angle was lower.

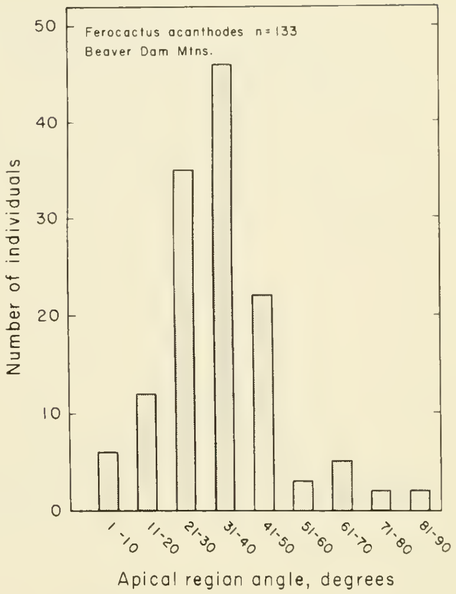

Fig. 3. Frequency histogram for inclination of the apical meristematic region of *Ferocactus acanthodes* in the Castle Cliffs population in the Beaver Dam Mountains, Utah.

An interesting feature of the temperature data was that in the winter apical region and south-facing tissue temperatures were much warmer during the day than those of the east-west facing tissues. The opposite pattern was observed in the summer. This pattern is explained by the changes in the declination of the sun between the two seasons. In the winter, when the sun was low in the sky, the apical region and south-facing tissue received more direct solar radiation and therefore heated more during the day. In the summer months, when the sun was higher overhead, it was the east-west-facing tissue that received greater intensities of solar radiation.

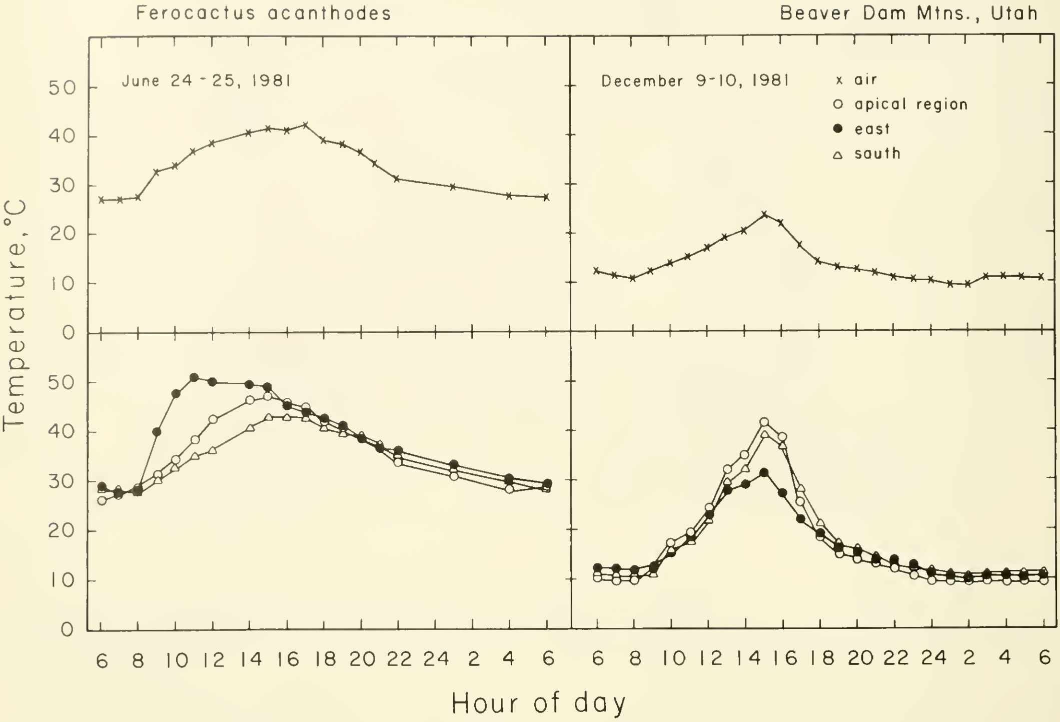

Fig. 4. Diurnal fluctuations in air and *Ferocactus acanthodes* tissue temperatures at Castle Cliffs 24–25 June and 9–10 December 1981.

Also consistent with both the summer and winter data sets was the observation that the apical region was cooler at night than other parts of the cactus and was usually cooler than air temperature. The significance of this observation will be discussed in the next section.

The micro-distributions of the barrel cactus were not uniform on all slopes. The cacti were found effectively only on slopes that faced south (Fig. 5). The density of barrel cactus ranged as high as 0.385 individuals m^{-2} on due-south-facing slopes, but quickly decreased to zero when slope azimuth deviated 60 degrees in either direction from south. On all slopes where the cactus density was greater than 0.06 individuals m^{-2}, the slope angles were inclined, ranging 20°–25°. In contrast, the slope angles at sites where the density was less than 0.06 were mostly less than 20°.

One aspect of the apparent restriction of barrel cactus to south-facing slopes was that the amount of solar radiation incident on these slopes during the winter was much higher than would occur on either a horizontal surface or on tilted slopes with different orientations. On a clear day at the winter solstice (December 21), the total daily amount of direct solar radiation incident on a horizontal slope would be approximately 8 MJ m^{-2}. From our observations, the barrel cactus did not occur on slopes with less than 11.5 MJ m^{-2} day^{-1} total solar radiation, and high densities of cacti did not occur until the total solar radiation exceeded 13 MJ m^{-2} day^{-1} (Fig. 6).

It seems likely that the size distributions of barrel cactus on slopes with contrasting orientations should be different. Unfortunately, the limited population sizes on non-south-facing slopes were so small that statistical analyses of frequency-size distributions could not be made.

Discussion

The distribution of the barrel cactus (*Ferocactus acanthodes* may be limited by two factors at its northern distribution limit: the ability of seedlings to become established (drought) and the ability of both seedlings and mature plants to avoid temperature extremes. These temperature extremes could

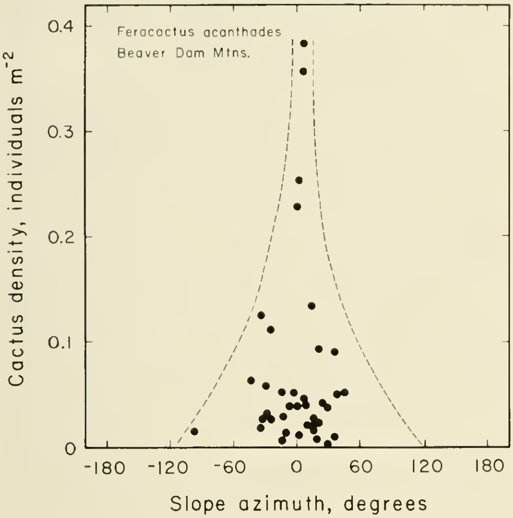

Fig. 5. Density of *Ferocactus acanthodes* as a function of the azimuth of the slope on which they occurred for the Castle Cliffs population in the Beaver Dam Mountains, Utah.

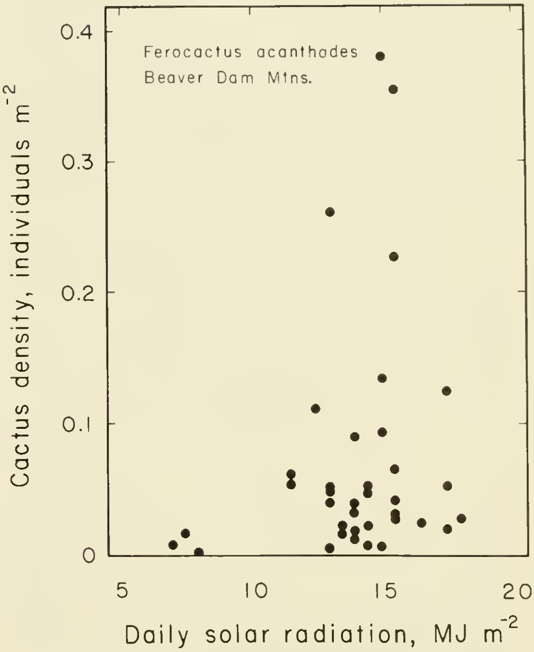

Fig. 6. Density of *Ferocactus acanthodes* as a function of the total daily amount of solar radiation incident on the slope surface for a clear day on the winter solstice for the population at Castle Cliffs in the Beaver Dam Mountains, Utah.

include low minimum tissue temperatures, which may cause freezing damage, as well as high tissue temperatures resulting in high rates of water loss and tissue desiccation.

Minimum tolerable tissue temperatures and the length of time an individual is exposed to subzero temperatures have been proposed by several authors as primary factors limiting the distributions of a number of desert cacti in southwestern North America (Shreve 1911, 1914, Turange and Hinckley 1938, Niering et al. 1963, Kincaide 1978). During low air temperature conditions, microsite distribution may play an important role in survival. South-facing slopes will receive greater heating by solar radiation during the cold winter months than any other slope orientation. As such, plants on south-facing slopes should be exposed to higher air temperatures and should additionally warm more because of the higher incident solar radiation heat loads. In this study, we observed that *F. acanthodes* were restricted to south-facing slopes and that the highest densities were on slopes with angles 20°–24°. The highest densities were found on those slopes that received greater heating during the winter months.

Ferocactus acanthodes also occurs throughout much of the Mohave and Sonoran deserts. Yeaton and Cody (1979) showed that the density of plants varied with microsite in those deserts as well. In particular, they found that in the warmest year-round site (Sonoran Desert) *F. acanthodes* were most common on south-facing slopes, but did occur in lesser amounts on east-west and north-facing slopes. At the cooler Mohave Desert sites, *F. acanthodes* occurred on east-west and south-facing slopes, but not on north-facing slopes. Thus, we see from these three sites a trend: as winter temperatures decrease, the barrel cactus decrease in density from the slopes that receive less winter solar heating.

Perhaps the most cold temperature-sensitive region of the barrel cactus is the apical region at the top of the cactus. Freezing temperature damage in this region will result in mortality, since stems are solitary. Nobel (1980a, 1980b, 1981) has shown that the minimum nighttime tissue temperature of the apical regions of columnar cacti species are up to several degrees cooler than the sides, because of the greater net long-wave radiation loss to the sky. The extent of nighttime cooling of the apical region will be a function of the surface area to volume ratio, so that the barrel cactus cools more slowly than the cylindrically stemmed *Opuntia* cactus. Our data corroborate these previous observations as nighttime tissue temperatures in the apical region were approximately 2 C cooler than the cactus sides, both in the winter and in the summer.

Since the apical region faced south, winter tissue temperatures should rise quickly during the day. The amount of solar radiation absorbed is accentuated by steep tissue angles, such as were observed in this study. As a consequence of this orientation, midday apical region tissue temperatures in the winter were as much as 19 C above air temperatures. Under subzero air temperatures, which may occasionally occur during the winter, the orientation of the apical region should result in tissue temperatures being above zero during the daytime hours. This would limit the time that the apical region was exposed to potentially low, lethal temperatures to the nighttime only.

Air temperature and relative humidites during the hot summer months will determine the evaporative demand imposed on the cactus. Jordan and Nobel (1981) showed that seedling establishment in *F. acanthodes* was restricted to wetter, cooler than average years, since in most years seedlings died of desiccation during the long summer drought. The globular shape observed in younger plants decreases the surface to volume ratio, thereby reducing the relative surface area exposed for transpiration. This also reduces the surface area for photosynthesis.

During the summer months, however, very little positive net photosynthesis occurs in these plants (Nobel 1977). The barrel cactus possesses CAM photosynthesis and during drought periods open their stomates at night for only a short time. Under prolonged drought these plants "idle" and do not open their stomates at all. Under these low photosynthesis conditions, Ehleringer et al. (1980) hypothesized that it may be advantageous for a cactus to orient such that the photosynthetic surfaces (sides of the cactus) received minimal amounts of solar radiation. This is what was observed in *F. acanthodes* where the body (stem) of the cactus was tilted at approximately 47° in a southerly direction. Such an orientation will minimize solar radiation incident on the sides of the cactus during the peaks of the drought period in the study area (September–October).

Cactus height distributions can help identify the periods of seedling establishment in a population (Shreve 1910, Brum 1973, Jordan and Nobel 1981, 1982). At our study site in the Beaver Dam Mountains, there was a single peak in height distribution at the 31–40 cm interval. Additionally, there was only a single individual observed to be less than 11 cm tall (it was 10 cm). Jordan and Nobel (1982) determined that the average yearly growth rate was a constant 9 mm yr^{-1} for *F. acanthodes*. Using this estimate, we calculate that no new barrel cactus plants have become established in the Beaver Dam population since approximately 1969 and that a major period of establishment was 1937–1947. Precipitation records for the region bear out that these were abnormally wet periods.

ACKNOWLEDGMENTS

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LITERATURE CITED

BENSON, L. 1982. The cacti of the United States and Canada. Stanford Univ. Press, Stanford.

BRUM, G. D. 1973. Ecology of saguaro (*Carnegia gigantea*): phenology and establishment in marginal populations. Madrono 22:195–204.

CAMPBELL, G. S. 1977. An introduction to environmental biophysics. Springer-Verlag, New York.

EHLERINGER, J., H. A. MOONEY, S. L. GULMON, AND P. W. RUNDEL. 1980. Orientation and its consequences for *Copiapoa* (Cactaceae) in the Atacama Desert. Oecologia 46:63–67.

JORDAN, P. W., AND P. S. NOBEL. 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. Ecology 62:901–906.

——. 1982. Height distributions of two species of cacti in relation to rainfall, seedling establishment, and growth. Bot. Gaz. 143:511–517.

KINCAIDE, T. B. 1978. The ecological distribution of cholla cactus (*Opuntia imbricata* (Haw.) DC) in El Paso County, Colorado. Southwestern Nat. 23:117–134.

LIST, R. J. 1966. Smithsonian meteorological tables. Smithsonian Inst. Press, Washington.

NIERING, W. A., R. H. WHITTAKER, AND C. H. LOWE. 1963. The saguaro: a population in relation to environment. Science 142:15–23.

NOBEL, P. S. 1977. Water relations and photosynthesis of a barrel cactus, *Ferocactus acanthodes*, in the Colorado Desert. Oecologia 27:117–133.

____. 1980a. Morphology, surface temperatures, and northern limits of columnar cacti in the Sonoran Desert. Ecology 61:1–7.

____. 1980b. Influences of minimum stem temperatures on ranges of cacti in southwestern United States and central Chile. Oecologia 47:10–15.

____. 1981. Influences on photosynthetically active radiation on cladode orientation, stem tilting, and height of cacti. Ecology 62:982–990.

SHREVE, F. 1911. The influence of low temperature on the distribution of the giant cactus. Plant World 14:136–146.

____. 1914. The role of winter temperatures in determining the distribution of plants. Amer. J. Bot. 1:194–202.

SHREVE, F., AND I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran Desert. Stanford University Press, Stanford.

TURNAGE, W. V., AND A. L. HINCKLEY. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. Ecol. Monogr. 8:529–550.

YEATON, R. I., AND M. L. CODY. 1979. The distribution of cacti along environmental gradients in the Sonoran and Mohave deserts. J. Ecology 67:529–541.

WALTER, H., AND E. STADELMANN. 1974. A new approach to the water relations of desert plants. Pages 213–310 *in* G. Brown, ed., Desert biology, vol. 2. Academic Press, New York.

ZAR, J. H. 1974. *Biostatistical analysis*. Englewood Cliffs, New Jersey: Prentice-Hall.

A SURVEY AND ASSESSMENT OF THE RARE VASCULAR PLANTS OF THE IDAHO NATIONAL ENGINEERING LABORATORY SITE

Anita F. Cholewa and Douglass M. Henderson[1]

ABSTRACT.— A two-year study of the rare vascular plants of the Idaho National Engineering Laboratory generated new data on the abundance, distribution, and habitat features of eight taxa presently under review at either the federal or state level, or recently proposed for such review. *Astragalus ceramicus* Sheld. var. *apus* Barneby is common on the INEL and adjacent areas and will be recommended for removal from further consideration at the federal level and placed on Idaho's Federal Watch List. *Coryphanta missouriensis* (Sweet) Britt. & Rose is common throughout east central Idaho , but will be recommended for retainment on the State Watch List. *Gymnosteris nudicaulis* (H. & A.) Greene and *Oxytheca dendroidea* Nutt. are also recommended for retention on the State Watch List. Four taxa not previously known to occur in Idaho or not known from the southeastern part of the state (*Astragalus gilviflorus* Sheld., *Astragalus kentrophyta* Gray var. *jessiae* (Peck) Barneby, *Gilia polycladon* Torr., and *Lesquerella kingii* S. Wats. var. *cobrensis* Roll. & Shaw) were encountered and evaluated with reference to current or potential threats, and are recommended for placement on Idaho's State Watch List.

Passage of the Endangered Species Act of 1973 and the subsequent reauthorizations have generated considerable interest in rare plant and animal taxa, especially among those federal agencies on whose lands these organisms occur. The multitude of questions from land managers concerning the status of rare plants, and the desire to know more about these unusual organisms, have resulted in the publication of numerous manuals generally summarizing data on a state-by-state basis (Henderson et al. 1977, Mozingo and Williams 1980, and others). Additionally, some federal agencies (e.g., U.S. Forest Service, BLM, U.S. Department of Energy) have contracted with botanists for surveys and assessments of the rare plants occurring on federal lands.

Although floristic studies have been accomplished on the U.S. Department of Energy Idaho National Engineering Laboratory (INEL) site (Atwood 1970, Jeppson and Holte 1978), they provided little information on the abundance and distribution of plant taxa inhabiting it, and additional studies would be necessary if accurate assessments of the rare plants were to be made. The U.S. Department of Energy, therefore, contracted with the University of Idaho for a survey and assessment of the rare vascular plants of the INEL.

Before any quantitative analysis of impacts on plants can be made, it is necessary to gather preliminary information on their abundance and distribution. Toward this major goal, field work on the INEL was initiated in the spring of 1981 with the following objectives: (1) document the abundance and distribution of all rare plant taxa occurring on the INEL, (2) assess subjectively current or potential threats to survival of the plants, and (3) make preliminary recommendations to the Department of Energy concerning the status and management of habitats supporting rare plant taxa.

STUDY AREA

The approximately one-half million acres of the INEL are located near the eastern end of the Snake River Plain in southeastern Idaho (Fig. 1). This is an area of lava flows and deep sand, with elevations ranging from 2004 m on East Butte to 1454 m in the Big Lost River Sinks. The vegetation is largely shrub-steppe, with *Artemisia tridentata* Nutt., *Chrysothamnus viscidiflorus* (Hook.) Nutt., *Agropyron spicatum* (Pursh) Scribn. & Smith, and *Poa secunda* Presl predominating, although woodlands of *Juniperus osteosperma* (Torr.) Little occur locally.

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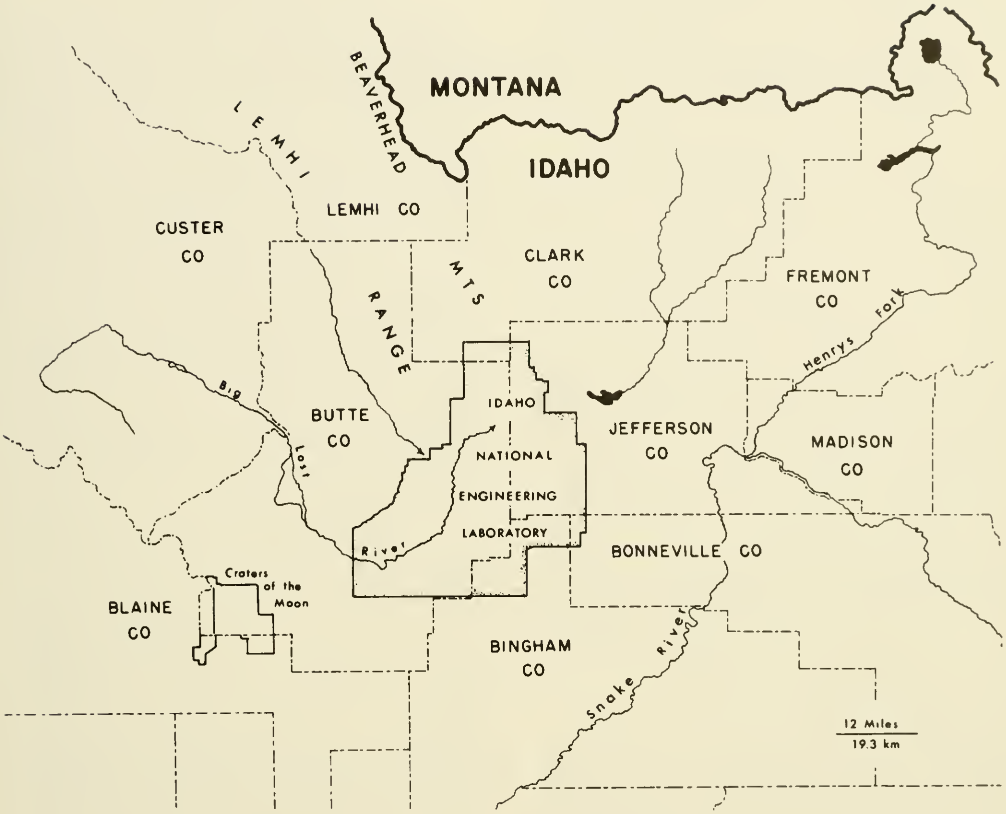
MONTANA
IDAHO
BEAVERHEAD MTS
LEMHI RANGE
LEMHI CO
CUSTER CO
CLARK CO
FREMONT CO
Henrys Fork
BUTTE CO
Big Lost River
IDAHO NATIONAL ENGINEERING LABORATORY
JEFFERSON CO
MADISON CO
BONNEVILLE CO
Craters of the Moon
BLAINE CO
BINGHAM CO
Snake River
12 Miles
19.3 km

Fig. 1. Location of Idaho National Engineering Laboratory.

METHODS

Since many rare plant taxa are known to be highly restricted to particular habitats, concentrated searching in suitable habitats is likely to be the most productive. Toward this objective, a tentative list of rare plant taxa was compiled to include known distribution, habitat, and phenological data. This list was generated largely from *The Vascular Plant Species of Concern in Idaho* (Rare and Endangered Plants Technical Committee, Idaho Natural Areas Council [INAC], 1981) and supplemented with recent data supplied by the herbaria of the College of Idaho (CIC), University of Idaho (ID), and Idaho State University (IDS).

Likely habitats were identified and located with the use of USGS topographic maps, a vegetation map of the INEL (McBride et al. 1978), assistance from INEL personnel, and prior personal experience within the area. These habitats were then searched intensively in two subsequent field seasons.

Upon encountering a species of concern, a subjective evaluation was made of population size and condition (including reproductive success), current or potential threats under existing management, and details of the habitat including associated species. Voucher specimens are deposited at ID, IDS, and the herbarium of the Radiological and Environmental Sciences Laboratory on the INEL.

RESULTS AND DISCUSSION

Four taxa from the tentative working list were encountered during the study, one of which is currently a candidate for federal review, and three are of state concern. No plant taxa currently established as either endangered or threatened at the federal or state levels were encountered on the INEL. Additional taxa not previously known from Idaho or which represented significant range extensions within Idaho, were also encountered. These taxa were evaluated in the same manner as taxa from the working list.

Candidate Taxa for Federal Review

Astragalus ceramicus Sheld. var. *apus* Barneby (Fabaceae).— Previously known as an inhabitant of dunes and other sandy places (Hitchcock et al. 1961, Barneby 1964), this taxon is endemic to the eastern end of the Snake River Plain. It was generally considered to be rare by members of the Rare and Endangered Plants Technical Committee, INAC (1981), although it was reported to be a co-dominant in sandy areas near the north end of the INEL (Anderson et al. 1978). This taxon is limited primarily to areas of moderate to deep sand and in communities with *Artemisia tridentata* ssp. *tridentata*, *Chrysothamnus viscidiflorus*, *Stipa comata* Trin. & Rupr., and *Oryzopsis hymenoides* (R. & S.) Ricker predominating.

Over 30 populations, each with numerous individuals, were encountered on the INEL during our study. Additional populations were also encountered in similar habitats adjacent to the INEL and in other areas of the eastern Snake River Plain.

Reproductive success appears to be moderate, with perhaps four to five legumes produced per aerial stem, and some seedlings were observed each season. Vegetative growth, however, through the production of extensive rhizomes, appears to be vigorous.

Nearly all populations examined are subjected to grazing by both cattle and sheep, although without definitive studies the impact of this activity on the populations remains largely unknown.

The apparent reproductive success, even with grazing, and the numerous populations supporting many thousands of individuals now known throughout the eastern Snake River Plain probably do not justify its status as a candidate for federal review. We have suggested instead that it be considered for placement on the state list of endemics or near endemics that do not appear to be in jeopardy, Idaho's Federal Watch List.

Idaho State Watch List Taxa

Astragalus gilviflorus Sheld. (Fabaceae).— Prior to its recent discovery in Idaho in 1981 by Goodrich (Goodrich et al. 1983), this species was known only as far west as Madison County, Montana. A single population is now known from a limestone ridge on the extreme southern end of the Beaverhead Mountains at Reno Point along the northeast border of the INEL. At this site there is virtually no soil development and the approximately 100 scattered plants are rooted in cracks in the bedrock within an open community of *Artemisia arbuscula* Nutt. var. *nova* (A. Nels.) Cronq., *A. tridentata* ssp. *wyomingensis* Beetle, *Poa secunda*, and *Petrophytum caespitosum* (Nutt.) Rydb. Close associates here include *Tanacetum nuttallii* T. & G., *Hymenopappus filifolius* Hook. var. *idahoensis* Turner, and *Penstemon aridus* Rydb.

Although this area is open to grazing, the rocky nature of the habitat and the extremely compact habit of *Astragalus gilviflorus* precludes any significant impact from grazing animals.

We have recommended to the Rare and Endangered Plants Technical Committee, INAC, that this taxon be placed on the State Watch List for Idaho, and suggest that additional similar habitats within this area be searched. Although its habit is distinctive, the plants can be easily overlooked.

Astragalus kentrophyta Gray var. *jessiae* (Peck) Barneby (Fabaceae).— This variety was reported to have a bimodal distribution with an eastern center in southwestern Wyoming and a western component in southwestern Idaho and adjacent Oregon (Barneby 1964). The variety was discovered on the INEL during the course of our study and was reported as a significant addition to its known range (Cholewa and Henderson 1983).

Only three small populations are now known from the eastern Snake River Plain, all within the INEL. The habitats are characterized by deep gravelly sand derived from highly erodable silicic volcanic deposits at the southern end of the Lemhi Range. The community here has been characterized as a *Juniperus osteosperma/Artemisia tridentata/Agropyron spicatum* vegetation type (McBride et al. 1978), but the sites supporting *Astragalus kentrophyta* var. *jessiae* are distinctive in lacking the *Artemisia*. Associated species include *Eriogonum ovalifolium* Nutt., *Arenaria franklinii* Dougl., and *Aristida purpurea* Nutt. var. *longiseta* (Steudel) Vasey.

It is clear from additional weedy species present and the obvious evidence of erosion that disturbance is a significant factor of this habitat. It is not clear, however, what influence the rather heavy grazing in the past has had on this taxon. For these reasons we have recommended placement of this taxon on the State Watch List for Idaho.

Coryphantha missouriensis (Sweet) Britt. & Rose (CACTACEAE).— Within the INEL this species appears to be restricted to gravelly flats and rocky ridges along the northern boundary in communities of *Artemisia tridentata* ssp. *wyomingensis* or *A. arbuscula* var. *nova*, both with *Poa secunda* as an important grass associate. Elsewhere in east central Idaho *Coryphantha missouriensis* is abundant.

No present threats to this species are apparent, although the possibility of future exploitation by cactus hunters prompted its placement on the State Watch List for Idaho.

Gilia polycladon Torr. (POLEMONIACEAE).— A member of the western Great Basin flora, its distribution in Idaho has been described only as "the sagebrush zones of s. w. Idaho" (Davis 1952), with no further data on specific locations. Its discovery on the INEL represents an extension to eastern Idaho (Cholewa and Henderson 1983).

Only a few locations are known for this taxon, on the INEL and on National Forest land to the northwest; all are on rocky slopes of volcanic or limestone origin. The communities are dominated by *Artemisia arbuscula* var. *nova* or *Elymus ambiguus* Vasey & Scribn. Close associates vary considerably among the areas but often include such taxa as *Langloisia setosissima* (T. & G.) Greene ssp. *punctata* (Cov.) Timbrook, *Lappula redowskii* (Hornem.) Greene, *Lupinus pusillus* Pursh, and *Cymopterus glaucus* Nutt.

Although the populations are located within areas open to livestock, the dry, rocky slopes probably prevent excessive grazing. We have recommended placement on Idaho's State Watch List until more data are available.

Lesquerella kingii S. Wats. var. *cobrensis* Roll. & Shaw (BRASSICACEAE).— This species is also a member of the Great Basin flora and was not known to occur in Idaho prior to our study. The var. *cobrensis*, formerly known only from the Pequop Range of Elko County, Nevada (Rollins and Shaw 1973), was discovered in the south central portion of the INEL (Cholewa and Henderson 1983). Habitats of the few Idaho populations are characterized by recent volcanics with extremely shallow soil. These open habitats are dominated by *Artemisia tridentata* ssp. *wyomingensis*, *Chrysothamnus viscidiflorus*, *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, and *Poa secunda*, with no apparent constant associates.

Although occurring in an area open to grazing, cattle may be excluded by the rocky nature of the habitat, but the full impact of livestock is presently unknown. Our recommendations, therefore, were placement on the State Watch List for Idaho and to search for additional populations.

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LITERATURE CITED

ANDERSON, J. E., R. J. JEPPSON, R. J. WILKOSZ, G. M. MARLETTE, AND K. E. HOLTE. 1978. Trends in vegetational development on the Idaho National Engineering Laboratory site. Pages 144-166 *in* Progress report Idaho National Engineering Laboratory site—ecology programs. IDO-12087. National Technical Information Service, Springfield, Virginia.

ATWOOD, N. D. 1970. Flora of the National Reactor Testing Station. Brigham Young Univ. Sci. Bull., Biol. Ser. 11(4). 46 pp.

AYENSU, E. S., AND A. DEFILIPPS. 1978. Endangered and threatened plants of the United States. Smithsonian Institution and World Wildlife Fund, Inc., Washington, D.C.

BARNEBY, R. C. 1964. Atlas of North American *Astragalus*. Mem. New York Bot. Gard. 13. 1188 pp.

CHOLEWA, A. F., AND D. M. HENDERSON. 1983. Noteworthy collections of Idaho: *Lesquerella kingii* var. *cobrensis*, *Astragalus kentrophyta* var. *jessiae*, and *Gilia polycladon*. Madroño 30:63–64.

DAVIS, R. J. 1952. Flora of Idaho. Brigham Young University, Provo, Utah. 836 pp.

GOODRICH, S., D. M. HENDERSON, AND A. F. CHOLEWA. 1983. Noteworthy collections of Idaho: *Astragalus gilviflorus* and *Hackelia davisii*. Madroño 30:63.

HENDERSON, D. M., F. D. JOHNSON, P. PACKARD, AND R. STEELE. 1977. Endangered and threatened plants of Idaho: a summary of current knowledge. Univ. of Idaho Forest, Wildlife and Range Expt. Sta. Contr. 73. 72 pp.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, AND J. W. THOMPSON. 1961. Vascular plants of the Pacific Northwest. Vol. 3. Univ. of Washington Press, Seattle. 614 pp.

JEPPSON, R. J., AND K. E. HOLTE. 1978. Flora of the Idaho National Engineering Laboratory site. Pages 129–143 *in* 1978 Progress report Idaho National Engineering Laboratory site—ecology programs. IDO-12087. National Technical Information Service, Springfield, Virginia.

MCBRIDE, R., N. R. FRENCH, A. H. DAHL, AND J. E. DETMER. 1978. Vegetation types and surface soils of the Idaho National Engineering Laboratory Site. IDO-12084. National Technical Information Service, Springfield, Virginia. 29 pp.

MONZINGO, H. N., AND M. WILLIAMS. 1980. Threatened and endangered plants of Nevada. USDI Fish & Wildlife Service and Bur. Land Management. 268 pp.

RARE AND ENDANGERED PLANTS TECHNICAL COMMITTEE, IDAHO NATURAL AREAS COUNCIL. 1981. Vascular plant species of concern in Idaho. Univ. of Idaho Forest, Wildlife and Range Expt. Sta. Bull. 34. 161 pp.

ROLLINS, R. C., AND E. A. SHAW. 1973. The genus *Lesquerella* (Cruciferae) in North America. Harvard Univ. Press. Cambridge, Massachusetts. 288 pp.

SUMMER FOOD HABITS OF A SMALL MAMMAL COMMUNITY IN THE PINYON-JUNIPER ECOSYSTEM

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ABSTRACT.— Summer food habits of a small mammal community in the Piceance Basin of Colorado were investigated during 1977 and 1978 using a combination of fecal and stomach content analyses. Three species, deer mice (*Peromyscus maniculatus*), least chipmunks (*Eutamias minimus*), and plains pocket mice (*Perognathus flavescens*) consumed arthropods as the majority of their diets. Bushy-tailed woodrats (*Neotoma cinerea*) consumed predominantly woody vegetation, and the diet of golden-mantled ground squirrels (*Spermophilus lateralis*) consisted primarily of forbs and fungi. Mountain cottontails (*Sylvilagus nuttalli*) depended heavily on grasses, with a mix of woody vegetation and forbs composing the remainder of their diet. Most of the species investigated selected different foods and thus avoided competition for food. Plains pocket mice may have competed with deer mice for arthropods in 1977.

The Piceance Basin of Colorado is an area where oil shale developments are occurring at a rapid rate. The food habits of small mammals occurring in the Piceance Basin are poorly understood. It is important to determine wildlife food habits so that wildlife foods and food chains can be considered in impact assessments. It was therefore considered important to investigate small mammal food habits and foraging relationships in the Piceance Basin. Food habits of deer mice (*Peromyscus maniculatus*), plains pocket mice (*Perognathus flavescens*), golden-mantled ground squirrels (*Spermophilus lateralis*), bushy-tailed woodrats (*Neotoma cinerea*), least chipmunks (*Eutamias minimus*), and mountain cottontails (*Sylvilagus nuttalli*) were investigated during the summers of 1977 and 1978.

STUDY AREA

The Piceance Basin covers an area of approximately 3500 km². It is a rolling uplands area consisting of approximately 32% upland sagebrush communities, 35% pinyon-juniper communities, 20% mixed mountain shrub communities, 3% bottomland sagebrush communities, and 9% other associations or uses (Wymore 1974). Mean annual precipitation is 406 mm, and the mean annual temperature is about 7 C (Wymore 1974).

The study area for this investigation was situated along the edge of a chained and a mature, unchained pinyon-juniper woodland (Sec. 3 and 9, T3S, R97W). The area had a slope of 5–10% on a northwesterly aspect at an elevation of 2100–2150 m. Chaining of the area, a process that involves dragging a heavy chain behind two bulldozers to knock down vegetation, was done 10 years prior to this study.

Vegetation on the study area was stratified into two types: the mature pinyon-juniper woodland and the chained area dominated by sagebrush and other shrubs. Vegetative cover was described by use of the line intercept method (Gysel and Lyon 1980). The edge between these two vegetation types was very narrow, lacking a discernible ecotonal area.

In the mature pinyon-juniper woodland, an overstory of pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) accounted for approximately 85% of the total vegetative cover of the area (Table 1). Shrubs in the understory accounted for 10% of the vegetative cover and included big sagebrush (*Artemisia tridentata*), Utah serviceberry (*Amelanchier utahensis*), alder-leaf mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), snowberry (*Symphoricarpus oreophilus*), and several species of rabbitbrush (*Chrysothamnus* spp.). A number of species of grasses and forbs composed the remaining 5% of the vegetative cover. Dominant grasses were western wheatgrass (*Agropyron smithii*), prairie junegrass (*Koeleria cristata*), needle-and-thread grass (*Stipa comata*), and downy brome (*Bromus tectorum*). The most abundant forbs included thistle (*Cirsium* sp.), prickly pear (*Opuntia polyacantha*), mallow (*Sphaeralcea coccinia*), fleabane (*Erigeron* sp.), and penstemon (*Penstemon* sp.). It should be noted that 1977 was an exceptionally dry year in the Piceance Basin (Rio Blanco Oil Shale Project 1978), reducing the relative amounts of grasses and forbs.

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Chained pinyon-juniper areas contained the same composition of plant species as the mature pinyon-juniper woodlands. Amounts of these species differed considerably, however. Pinyon pine and Utah juniper composed only 21% of the vegetative cover (Table 1). Shrubs composed approximately 63% of the vegetative cover, with big sagebrush, Utah serviceberry, and snowberry the most abundant species.

METHODS

Food habits of selected species were determined in both 1977 and 1978 by the use of fecal analysis. Scats for the fecal analyses were collected from first-time captures of animals in live traps located throughout the study area during June and July. Collected scats were dried and stored in envelopes until analysis. In addition, food habits of selected species were determined by the use of stomach content analyses in June 1978. Selected species were collected by trapping or shooting, and their stomach contents were removed and frozen. Both fecal and stomach content analyses were conducted at the Composition Analysis Laboratory in the Department of Range Science at Colorado State University.

Fecal analysis is a procedure in which plant fragments in the feces of herbivores are microscopically identified. Arthropod parts in the feces of an animal can also be identified in this process using lower magnification. The Sparks and Malechek method (1968), using microscopic techniques for estimating percentage of dry weight expressed as percent relative density of each item in a diet, was utilized by the Composition Analysis Laboratory.

Analysis of omnivore feces in 1977 utilized a two-stage analysis. The first stage identified arthropods in the diet using a chosen number of low magnification "fields." The second stage of the analysis used a chosen number of high-power "points" for the identification of plant species.

In 1977 both fields and points were used in sample analyses. In 1978 only the high-power point analysis was used in the fecal analyses. This provided information on amounts of plant species and on the total amounts of arthropods in each diet, but did not break down the arthropod component. Stomach contents of animals collected in 1978 were also analyzed for composition of food items using the point analysis.

Chipmunk food habits were to be determined in both 1977 and 1978, but small chipmunk populations during the sampling period made it unfeasible to collect an adequate sample size in 1978.

Means and standard errors were determined for all food items. Stomach contents and fecal samples were compared by the use of a t test to determine important food items in the diet of deer mice. Comparisons were also made between deer mice food habits in 1977 and 1978.

RESULTS

In 1977, 72 fecal samples from deer mice were collected. These were combined into 24 composite fecal samples of 3 deer mice each. Similarly, fecal samples from 60 least chipmunks were combined to make 20 composite fecal samples of 3 least chipmunks each. Twelve individual fecal samples from golden-mantled ground squirrels were analyzed, as were 8 individual fecal samples from bushy-

TABLE 1. Percent cover of vegetation categories in vegetation types sampled in the Piceance Basin, Colorado, July 1977. Cover values are means and standard errors.

Study area	Unchained pinyon-juniper woodland	Chained area
Grasses	1.23 ± 0.12	1.94 ± 0.17
Forbs	0.94 ± 0.60	0.67 ± 0.10
Shrubs	4.33 ± 0.66	10.44 ± 1.06
Trees	37.69 ± 2.01	3.56 ± 0.54

tailed woodrats and 10 individual fecal samples from plains pocket mice. Means and standard errors of all food items comprising at least 1.0% of the diet of these five species are listed in Table 2. Arthropods identified in the feces of the omnivorous species (deer mice, least chipmunks, plains pocket mice, and golden-mantled ground squirrels) are listed in Table 3.

Stomach contents from 1978 sampling were analyzed for 43 deer mice, 10 cottontails, and 8 golden-mantled ground squirrels. In addition, 62 composite fecal samples of 3 deer mice each were analyzed in 1978.

In 1978, only two food items were found to compose more than 1.0% of the diet of deer mice based on either fecal or stomach analyses. Fecal analyses revealed that arthropods composed 95.8% of the diet of deer mice, with a standard error of 1.0%. Seeds composed 1.60 ± 0.9% (mean and standard error) of the diet based on fecal analyses. Analyses of stomach contents indicated that 83.8 ± 2.4% of the diet was arthropods, and 14.5 ± 2.4% of the diet was seeds. Comparisons of fecal to stomach contents by the use of a t test revealed that estimates of both arthropods and seeds in the diets were different ($p<0.001$). In addition, arthropod and seed estimates determined by fecal analysis were compared between 1977 and 1978. No difference was found in seeds ($p>0.05$), but arthropod estimates were lower in 1977 than in 1978 ($p<0.01$).

Major food items identified in the stomach contents of cottontails and golden-mantled ground squirrels in 1978 are listed in Table 4.

Discussion

In 1977 the diet of deer mice consisted predominantly of arthropods. No other food item composed more than 2.0% of the diet, as determined by fecal analysis. Although past investigations have identified insects as important foods of deer mice, especially in the

Table 2. Food habits as determined by fecal analysis of selected small mammals sampled during July–August 1977 in the Piceance Basin, Colorado. Values are means and standard errors of percent relative density of food items accounting for more than 1.0% of the diet of a species.

Food item	Deer Mice N = 24	Chipmunks N = 20	Bushy-tailed woodrat N = 8	Plains pocket mice N = 10	Golden-mantled ground squirrel N = 12
Grasses					
Agropyron					1.5 ± 1.5
Koeleria					2.7 ± 2.7
Stipa					1.1 ± 1.0
Bromus				2.9 ± 2.0	
Forbs					
Astragalus			1.5 ± 0.9		6.2 ± 3.9
Erigeron		2.8 ± 1.0	1.2 ± 0.7		6.4 ± 2.7
Cirsium	1.1 ± 0.6	6.1 ± 2.2			31.2 ± 11.0
Phlox				5.1 ± 4.8	
Spaeralcea			11.5 ± 5.1		2.9 ± 1.2
Balsamorhiza					3.9 ± 2.5
Opuntia		1.9 ± 1.9			
Woody vegetation					
Purshia tridentata			65.5 ± 4.2		16.6 ± 6.8
Artemisia		1.3 ± 0.5			
Symphoricarpos			10.2 ± 4.2		
Cercocarpus	1.1 ± 0.3	2.2 ± 1.5			
Amelanchier					9.0 ± 3.7
Quercus				3.2 ± 3.2	
Pinus	1.3 ± 0.3	4.0 ± 0.9	2.3 ± 2.0	3.2 ± 2.1	
Juniperus	1.0 ± 0.3	4.3 ± 1.2	4.4 ± 1.7	16.8 ± 9.0	
Lichen		1.3 ± 0.7			6.3 ± 5.6
Moss	1.7 ± 0.4	2.2 ± 0.8		1.6 ± 1.6	
Seed				3.5 ± 2.1	1.5 ± 0.8
Arthropods	90.8 ± 1.5	70.6 ± 3.1		59.5 ± 12.7	7.3 ± 1.9

spring, only Jameson (1952) found insects composing a comparable amount of the diet of deer mice. Shepard (1972), investigating deer mice food habits in the pinyon-juniper ecosystem, reported insects to compose about 62% of the diet of deer mice in the spring and summer. Goodwin and Hungerford (1979) found that deer mice ate 13% insects and 70% forbs in the ponderosa pine ecosystem. It was first hypothesized that the high level of arthropods in the diet of deer mice in 1977 might have been caused by dry conditions that year and a corresponding lack of seed production. Growth of grasses and forbs was very poor, with many species failing to flower or seed. Analysis of deer mice food habits in 1978, a more normal year in terms of precipitation, discredited this hypothesis. Deer mice consumption of arthropods in 1978 was significantly greater than in 1977, even though abundant amounts of seeds and vegetation were present. Johnson (1961), Shepard (1972), and Vaughan (1974) reported that insects were the preferred diet of deer mice when available, which agrees with the findings of this study.

In 1978 arthropods composed about 84% of the diet of deer mice as determined by stomach content analysis. This amount was significantly lower than the percentage identified in the fecal analysis. Thus it appears that fecal analysis may overemphasize the importance of arthropods in the diet, because the stomach contents were felt to be a more accurate sampling method than the fecal samples. Stomach contents composed of 84% arthropods, however, still reflect a large amount compared to other studies. It may be that the large amount of slash present in the study area in the Piceance Basin supported sizable arthropod populations, increasing deer mice use of these food items. The high percentage of Coleoptera and Formicidae identified in the diet of the deer mice in 1977 would support this explanation.

In 1977 chipmunks depended heavily on arthropods. Like the deer mice, they ate a high percentage of Coleoptera. They ate appreciably more Lepidoptera larvae than deer mice, however. This may have reflected the availability of arthropods during the period when the diurnal chipmunks were most active as opposed to when the nocturnal deer mice were most active. This difference may also have been influenced by the different foraging areas of deer mice and chipmunks reported by Johnson (1961). The high percentage of arthropods eaten by chipmunks may have been caused by the scarcity of plant foods due to the dry conditions in 1977 (approximately 30% of their diet was composed of plant matter in 1977). The number and amount of plant species eaten support Vaughan's (1974) observation that chipmunks were a more generalized feeder than deer mice.

Table 3. Important orders of arthropods in the diets of omnivorous small mammals during July–August 1977 in the Piceance Basin, Colorado. Values are means and standard errors of percent relative density of food items.

	Deer mice	Chipmunks	Plains pocket mice	Golden-mantled ground squirrel
Sample size	24	20	10	12
Total percentages in the diet	90.8 ± 1.5	70.6 ± 3.1	59.5 ± 12.7	7.3 ± 1.9
	Relative density of arthropods			
Class Arachnida				
Order: Araneida	2.1 ± 0.4	0.1 ± 0.1		
Class Insecta				
Order: Coleoptera	53.0 ± 4.9	52.2 ± 5.8	11.2 ± 9.9	6.3 ± 4.1
Order: Hymenoptera				
Family: Formicidae	21.3 ± 4.4	2.3 ± 0.9	2.1 ± 1.1	8.9 ± 4.8
Others	2.1 ± 1.1	3.9 ± 1.3	11.9 ± 8.7	11.6 ± 8.0
Order: Lepidoptera	13.8 ± 2.9	25.5 ± 4.3	30.0 ± 13.5	
Order: Orthoptera	4.6 ± 0.8	8.1 ± 3.2	2.4 ± 2.4	
Other insects	0.1	0.2	11.5	10.6
Plant material	2.5 ± 0.7	7.9 ± 4.0	30.8 ± 26.4	55.7 ± 20.6
Hair				6.8

Plains pocket mice were also found to consume a large percentage of arthropods in 1977. This result is contrary to the seed-eating food habits usually attributed to pocket mice (Martin et al. 1951). In 1977 they were found to eat 59% arthropods, based on fecal analysis. Undoubtedly, the lack of seed production in 1977 influenced the food habits of this species, and may have caused increased competition for food between the pocket mice and deer mice and chipmunks.

Golden-mantled ground squirrel diets were determined for both 1977 and 1978. Statistical comparisons between the two years were not deemed valid, however, because fecal analysis was used in 1977 and stomach content analysis was used in 1978.

In 1977, golden-mantled ground squirrels depended heavily on the relatively few types of forbs available. Thistle, a fairly drought-tolerant plant, was available in 1977. This plant composed about 30% of the diet of ground squirrels as indicated by fecal analysis. Bitterbrush also was consumed in large amounts. Arthropods composed only about 7% of the diet of the ground squirrels. This diet was similar to that reported by Goodwin and Hungerford (1979), with the exception of the bitterbrush component.

In 1978 the diet determined for golden-mantled ground squirrels was quite different than that determined for 1977. Fungi composed about 64% of the stomach contents. No fungi were identified in the feces in 1977. Two reasons could explain this. First, fungi are readily digested and are therefore hard to distinguish in feces. Alternatively, the drought conditions in 1977 would preclude the growth of most fungi, making them unavailable as a food; growing conditions in 1978 were more favorable.

TABLE 4. Food items composing greater than 1.0% of identified stomach contents of cottontails and golden-mantled ground squirrels collected in the Piceance Basin, Colorado, during June 1978. Values are means and standard errors of percent relative densities determined by high-power microscopic analysis.

Food item	Cottontail N = 10	Golden-mantled ground squirrel N = 8
Bromus	30.7 ± 2.9	
Carex	4.1 ± 1.3	
Oryzopsis	1.0 ± 0.5	
Poa	2.8 ± 1.3	
Stipa	8.4 ± 3.9	
Amelanchier	17.3 ± 5.0	
Antennaria	2.2 ± 1.6	6.2 ± 6.2
Astragalus	10.4 ± 2.7	8.0 ± 6.8
Crepis		2.1 ± 2.1
Erigeron	1.5 ± 0.5	
Flower parts		6.6 ± 6.6
Fungus		64.1 ± 13.9
Lupinus		5.3 ± 3.6
Sphaeralcea	14.6 ± 6.6	
Unknown forb	2.4 ± 1.4	
Arthropod		6.3 ± 4.5

Forbs were a preferred food of ground squirrels in the Piceance Basin, with woody vegetation apparently of low palatability but eaten to some extent. Tevis (1952) reported seeds as an important component of the diet, as did Martin et al. (1951), but these were not identified as a major food item in this investigation, composing only about 1% of the diet. McKeever's (1963) findings were similar to those of this investigation. Arthropods have been reported to be a small but consistent component of the diet of golden-mantled ground squirrels, a finding supported by the results of both years of this investigation.

Bushy-tailed woodrats were found to be herbivorous, eating plant foods even in the dry year of 1977. This supports the findings of Findley (1958). In 1977 woody plants accounted for over 75% of the diet, with bitterbrush being the predominant food item identified. Forbs were also eaten, but composed less than 15% of the diet in 1977. It is possible that in years with more rainfall than 1977 had, a greater amount of forbs might be eaten. By eating woody vegetation, however, bushy-tailed woodrats may avoid competition with other forb-eating small mammals.

Cottontail rabbits were herbivorous, depending upon grasses for nearly half their diet in 1978. Forbs and serviceberry composed the remainder of their diet. These foods would not place cottontails in significant competition with the other small mammals.

CONCLUSION

Most of the species investigated appeared to avoid competition for food by selecting different food items as the main component of their diets. A possible exception was the arthropod component of the diet of plains pocket mice. The dry condition in 1977 may have caused this species to depend more heavily on arthropods than on its expected diet of seeds, and thus placed it in increased competition with deer mice. Additional investigation of the foraging relationship of these two species under varying climatic conditions would be necessary to determine if serious competition could occur in some situations.

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LITERATURE CITED

FINDLEY, R. B., JR. 1958. The wood rats of Colorado: distribution and ecology. Univ. of Kansas Publ., Mus. of Nat. Hist. 10:213–552.

GOODWIN, J. G., JR., AND C. R. HUNGERFORD. 1979. Rodent population densities and food habits in Arizona ponderosa pine forests. USDA For. Serv. Res. Paper RM-214. 12 pp.

GYSEL, L. W. AND L. J. LYON. Habitat analysis and evaluation. Pages 305–327 *in* S. D. Schemnitz, ed., Wildlife management techniques manual. Wildlife Soc., Washington, D.C. 686 pp.

JAMESON, E. W., JR. 1952. Food of deer mice, *Peromyscus maniculatus*, and *P. boylei*, in the northern Sierra Nevada, California. J. Mammal. 33:50–60.

JOHNSON, D. R. 1961. The food habits of rodents in range lands of southern Idaho. Ecology 42:407–410.

MARTIN, C., S. ZIM, AND L. NELSON. 1951. American wildlife and plants, a guide to wildlife food habits. Dover Publ., Inc. New York. 500 pp.

MCKEEVER, S. 1964. The biology of the golden-mantled ground squirrel, *Citellus lateralis*. Ecol. Monogr. 34:383–401.

RIO BLANCO OIL SHALE PROJECT. 1978. Modular development phase in monitoring, report 1. Vol. 1 of 2. Sept. 1977–Nov. 1977, year end rept. Gulf Oil Corp. and Standard Oil Co. (Indiana). 114 pp.

SHEPARD, H. R. 1972. Rodent effects on pinyon-juniper deer range. Co. PR Proj. W-101-R-14. 70 pp.

SPARKS, D. R., AND J. C. MALECHEK. 1968. Estimating percentage dry weights in diets using a microscopic technique. J. Range Mgmt. 21:264–265.

TEVIS, L., JR. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels. J. Mammal. 33:206.

VAUGHAN, T. W. 1974. Resource allocation in some sympatric subalpine rodents. J. Mammal. 55:764–795.

WYMORE, I. F. 1974. Estimated annual water balance for Piceance and Yellow Creek watersheds. Tech. Rept. Series 2. Environmental Resources Center, Colorado State Univ., Fort Collins. 60 pp.

NODULATION AND ACETYLENE REDUCTION BY TWO LEGUMES WITH RHIZOBIA INDIGENOUS TO NORTHERN GREAT BASIN SOILS[1]

M. D. Rumbaugh[2] and D. A. Johnson[2]

Abstract.— *Medicago sativa* L. and *Hedysarum boreale* Nutt. were grown in the greenhouse on soils representing 27 of the major soil associations of the northern Great Basin. Nodulation of *Medicago sativa* L. by indigenous rhizobia occurred with 25 of the soil associations and of *Hedysarum boreale* Nutt. with 21 of these soil associations. Nitrogen fixation, as indicated by acetylene reduction activity, was greater for *Medicago sativa* L. than for *Hedysarum boreale* Nutt. for most of the soil associations. Multiple regression functions incorporating 49 independent climatic, edaphic, and vegetation variables failed to predict acetylene reduction activity with satisfactory precision.

Forage yield and quality have been increased on some range sites by including legumes in reseeding mixtures (Rumbaugh et al. 1982) or by interseeding them into existing vegetation (Lorenz 1982). Alfalfa (*Medicago sativa* L.) and yellow-blossom sweetclover (*Melilotus officinalis* L.) can maintain satisfactory stand densities by reseeding on some range sites (Nichols and Johnson 1969, Rumbaugh 1982). Although legume seeds can be inoculated with selected, highly efficient nitrogen-fixing strains of *Rhizobium* species prior to planting, the fate of the bacteria has not been determined in arid and semiarid range ecosystems. *Rhizobium meliloti* Dang. strains considered to have potential for inoculant production differed markedly with regard to their competitive abilities on *M. sativa* (Van Rensburg and Strijdom 1982). Not all the strains identified as the better competitors in autoclaved soils were able to satisfactorily nodulate alfalfa plants in a South African field soil containing an established population of *R. meliloti*. Introduced strains of bacteria added to some soils were destroyed rapidly by antagonistic organisms (Katznelson 1940, Waksman and Woodruff 1940). Numbers of *R. meliloti* in alfalfa hay fields decline with increasing age of stands (Barber 1980). Thus, rangeland legumes may be dependent upon indigenous *Rhizobium* populations for inoculation and nitrogen fixation at the time they are first planted or in later generations if they are capable of reseeding.

The objectives of our study were to determine (1) whether or not soils of the northern Great Basin contained indigenous *Rhizobium* strains capable of nodulating *Hedysarum boreale* Nutt. and *M. sativa*, (2) the effectiveness of such strains for nitrogen fixation as indicated by acetylene reduction activity, and (3) the usefulness of easily measured or recognized climatic, edaphic, and vegetative factors for predicting the presence or absence of effective *Rhizobium* populations in rangeland soils of the study area.

Materials and Methods

Soil samples were collected during 7 to 12 June 1982 from 85 sites representing 27 of the major soil associations of the northern Great Basin (Table 1). Collection sites (Fig. 1) were located and identified with the aid of soil association maps and descriptions (Wilson et al. 1975). A 2-kg soil sample from the upper 15 cm of the profile was extracted from 5 areas at each site. The five samples from each site were bulked, placed in a polyethylene bag, sealed, labeled, and returned to the laboratory for pH measurement and subsequent refrigeration. Sites were characterized as being cropland or noncropland and the dominant native or introduced plant species were identified. The mean annual precipitation and the summer and annual soil temperatures for each association were also recorded (Wilson et al. 1975).

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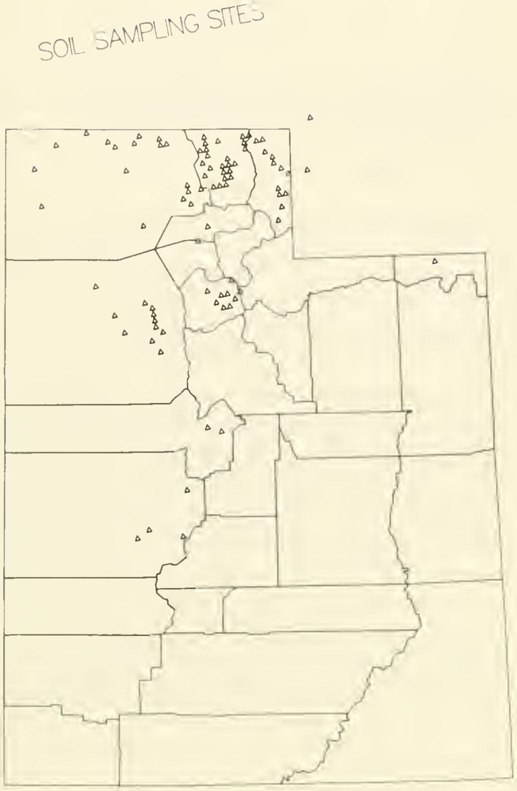

Fig. 1. Approximate locations of the 85 soil sampling sites, mostly within the state of Utah.

An experimental population of northern sweetvetch (*H. boreale* Nutt.), which is native to the study region, and 'Spredor 2' alfalfa, an introduced species widely cultivated throughout the Great Basin, were used as macrosymbiont legume hosts.[3] Seeds were mechanically scarified, surface sterilized by immersion in 95% ethyl alcohol for 15 minutes (Jing et al. 1982), and germinated in sterile plastic boxes containing absorbent blotters wetted with tap water. One-week old seedlings were transplanted the first week of July into previously unused, chlorine-treated plastic containers (3.8 cm diameter at the top and tapered over the 21 cm length to a 2.5 cm diameter at the bottom). These containers were filled with soils of the 85 samples that had been screened for pebbles and detritus particles larger than approximately 5 mm diameter. Plants of the two species were grown in the greenhouse in two adjoining locations, with no supplemental lighting. Experimental designs were randomized complete blocks with four replications each. During 27 to 29 September 1982, the plants were removed from the containers and the roots gently washed over fine-meshed screens to remove the soil particles without dislodging the nodules. The shoots of the plants were excised, oven dried, and weighed. Intact roots and attached nodules were used to measure acetylene reduction activity. The procedures followed were similar to those previously described by Johnson and Rumbaugh (1981) except that the intact root systems were incubated one hour in 60-cc plastic syringes. Oven-dry root and nodule weights and nodule numbers were subsequently obtained for each plant. Data were analyzed by analysis of variance, chi-square, and multiple regression.

Results and Discussion

Nodulation

Fifty-five percent of the alfalfa plants had one or more nodules on their roots, whereas only 32% of the sweetvetch plants were nodulated (Table 2). Despite the fact that sweetvetch is native to the northern Great Basin area and alfalfa is not, indigenous rhizobia were able to nodulate alfalfa more frequently than sweetvetch. Although the absolute nodulation frequencies varied depending upon whether or not the soil collection sites had been cropped, on both cropland and noncropland, alfalfa was nodulated more often than sweetvetch. Twenty-two of the 85 soils samples were from sites currently being used for crop production. On cropland, 68% of the alfalfa and 39% of the sweetvetch plants were nodulated. On noncropland, corresponding frequencies were 53% for alfalfa and 31% for sweetvetch. In both cases the chi-square tests of homogeneity between species were highly significant ($P<0.01$).

All alfalfa plants grown in the soil samples from associations 33, 35, 45, 50, and 67 were

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[3] Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the USDA and does not imply its approval to the exclusion of other products or vendors that may be suitable.

Table 1. Soil description, dominant species in climax vegetation, and number of sites sampled and tested for each of 27 soil associations.*

Association number	Soils	Soil description	Dominant species in climax vegetation**	Number of sites sampled
1	Argic Cryoborolls–Pachic Cryoborolls–Cryic Paleborolls Association	High mountain loams and stony loam	Bigtooth maple, slender wheatgrass, quaking aspen, blue wildrye, Douglas fir	15
9	Lithic Argiborolls–Rock outcrop–Typic Argiborolls Association	Mountain loams and mountain gravelly and stony loams	Gambel oak, birchleaf mountain mahogany, mountain brome, bearded wheatgrass	1
21	Typic Argixerolls–Cumulic Haplaquolls Association	Mountain loams, mountain stony loam, upland stony loam, and wet meadow soils	Gambel oak, bearded wheatgrass, bluebunch wheatgrass, big sagebrush, tufted hairgrass, sedges	5
22	Typic Argixerolls–Typic Haploxerolls Association	Mountain loams, mountain stony or gravelly loams, and mountain stony clay soils	Gambel oak, bluebunch wheatgrass, slender wheatgrass, basin wildrye	5
23	Calcic Haploxerolls–Calcic Argixerolls Association	Mountain or upland loams and stony loams	Bluebunch wheatgrass, basin wildrye, big sagebrush, black sagebrush, shadscale	2
24	Lithic Haploxerolls–Typic Haploxerolls Association	Mountain loam, mountain stony, gravelly, or shallow loams	Bluebunch wheatgrass, Gambel oak, curlleaf mountain mahogany, antelope bitterbrush	6
25	Pachic Argixerolls–Typic Argixerolls–Calcic Argixerolls Association	Mountain loams and mountain gravelly or stony loams	Bluebunch wheatgrass, bearded wheatgrass, Gambel oak, basin wildrye, big sagebrush	1
26	Calcic Argixerolls–Calcic Haploxerolls Association	Cropland		5
27	Typic Calcixerolls–Calcic Argixerolls Association	Cropland		2
28	Aquic Calciustolls–Typic Calciaquolls–Fluvaquentic Haplustolls Association	Cropland		7
29	Aridic Calcic Argixerolls–Aridic Haploxerolls Association	Upland loams and upland stony loam	Bluebunch wheatgrass, Utah juniper, antelope bitterbrush	1
30	Lithic Argixerolls–Aridic Haploxerolls–Aridic Calcixerolls Association	Upland loam and upland stony or shallow loams	Bluebunch wheatgrass, Utah juniper, big sagebrush	1
31	Aridic Calcixerolls–Xerollic Calciorthids Association	Upland loam and upland stony loam	Bluebunch wheatgrass, black sagebrush, big sagebrush, antelope bitterbrush	2

*Adapted from Wilson, et al. 1975. Soils of Utah.

**See Appendix for a listing of the scientific names of these plant species.

Table 1 continued.

Association number	Soils	Soil description	Dominant species in climax vegetation**	Number of sites sampled
33	Aridic Calcic Argixerolls–Aridix Petrocalcic Palexerolls Association	Upland loam, upland stony loam, and upland shallow hardpan soils	Bluebunch wheatgrass, Utah juniper, black and big sagebrush, antelope bitterbrush	1
34	Aridic Calcixerolls–Xerollic Calciorthids Association	Upland loam and upland stony and gravelly loams	Bluebunch wheatgrass, big sagebrush, Utah juniper	2
35	Ustic Torrifluvents–Borollic Calciorthids Association	Upland loam or upland stony loams	Bluebunch wheatgrass, big sagebrush, antelope bitterbrush	1
39	Ustollic Haplargids–Ustollic Calciorthids Association	Semidesert loam and semidesert stony hill soils	Bluebunch wheatgrass, Indian ricegrass, needle and thread, big sagebrush	1
43	Aquic Calciorthids–Aquic Ustifluvents Association	Wet or semiwet meadows and semiwet stream bottoms	Sedges, tufted hairgrass, slender wheatgrass bitterbrush	2
44	Xerollic Calciorthids–Xeric Torriorthents Association	Semidesert loam and semidesert gravelly loam	Bluebunch wheatgrass, big sagebrush, black sagebrush	5
45	Xerollic Calciorthids–Xerollic Paleorthids Association	Upland loam, semidesert shallow or gravelly loams, and semidesert shallow hardpan soils	Bluebunch wheatgrass, big sagebrush, Utah juniper	1
47	Xerollic Haplargids–Xerollic Calciorthids Association	Upland or semidesert, semidesert silt or limy, and upland stony loams	Bluebunch wheatgrass, big sagebrush, black sagebrush	7
48	Xeric Torrifluvents–Xerollic Calciorthids Association	Upland or semidesert, semidesert silt or limy, and upland stony loams	Bluebunch wheatgrass, big sagebrush, bottlebrush squirreltail	4
50	Lithic Xerollic Calciorthids–Xerollic Calciorthids Association	Semidesert shallow or limy loams	Bluebunch wheatgrass, black sagebrush, big sagebrush, bottlebrush squirreltail	1
60	Typic Natrargids–Xerollic Natrargids–Typic Calciorthids Association	Semidesert or desert salt and alkali flats and bench soils	Winterfat, shadscale, greasewood, Nuttall saltbush	2
62	Typic Natrustalfs–Typic Natrquolls Association	Semidesert alkali flats and bottoms and salt meadow soils	Bottlebrush squirreltail, greasewood, shadscale, western wheatgrass, Nuttall saltbush	5
67	Ustic Torripsamments Association	Upland sands	Utah juniper, pinyon pine, greenleaf manzanita, big sagebrush	1
71	Playas			2

*Adapted from Wilson, et al. 1975. Soils of Utah.

**See Appendix for a listing of the scientific names of these plant species.

nodulated. Similarly, all plants of sweetvetch grown on soils of associations 25 and 35 were nodulated. All of these soils except for association 67 were mountain upland, or semidesert loams supporting growth of bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn. & Smith) and various sagebrush species (*Artemisia*) as dominant components of the climax vegetation. Even soil association 67, which is an upland sand, has big sagebrush (*Artemisia tridentata* Nutt.) as a dominant species in the climax vegetation. However, 5 of the 6 associations in which either legume was not nodulated also were loam soils supporting populations of bluebunch wheatgrass and big sagebrush. Although Hely and Brockwell (1962) noted that *R. meliloti* populations were positively correlated to density of native grass species in Australia, this pattern was not apparent in soils of the northern Great Basin.

Soil pH ranged from 6.1 to 8.5 and averaged 7.3 in the 85 soil samples used in our study. Even at the lowest pH, 50% of the plants of each of the two macrosymbionts were nodulated. Soil pH can greatly affect population levels of rhizobia. For example, Sagardoy (1981) found that much of the variation in number of *R. meliloti* in soils near Buenos Aires was dependent on soil pH. Barber (1980), Nutman and Ross (1970), and Rice et al. (1977) also reported that hydrogen ion activity could be a major factor restricting the number of rhizobia in soils. In our study, correlation of pH with nodule number per alfalfa plant was $r=0.08$ and with nodule dry weight, $r=0.03$. Coefficients for sweetvetch were of similar magnitude, with $r=0.09$ and $r=-0.01$ for nodule number and dry weight, respectively. The differences in the results of these studies probably were due to the lower pH values of the soils they studied compared to those of the Great Basin.

Sagardoy (1981) found that 79 of the 86 soil samples he investigated contained alfalfa root-nodule bacteria, and about 16% of the

TABLE 2. Frequency of nodulation of two legumes grown on soils from 27 major soil associations of the northern Great Basin.

Independent variable	No. of plants	Avg. pH	Frequency of nodulation (%) *Hedysarum boreale*	Frequency of nodulation (%) *Medicago sativa*	Probability of homogeneity between species (%)
SPECIES	678	7.29	32	55	0[*]
LAND USE					
Cropland	111	7.47	39	68	1
Noncropland	567	7.26	31	53	0
SOIL ASSOCIATIONS					
1	120	6.43	18	47	0
9	8	7.82	25	75	49
21	16	7.41	0	12	100
22	40	7.25	55	50	100
23	16	6.92	50	62	100
24	48	7.40	58	54	100
25	8	6.90	100	50	43
26	41	7.44	30	62	8
27	16	7.74	38	50	100
28	55	7.64	36	48	51
29	8	7.30	50	25	100
30	8	7.56	0	0	100
31	16	7.09	25	75	13
33	8	7.82	0	100	3
34	16	7.36	88	75	100
35	8	7.93	100	100	100
39	8	7.32	0	50	43
43	16	7.08	0	50	8
44	39	7.57	55	53	100
45	8	7.61	0	100	3
47	56	7.26	11	54	0
48	32	7.87	38	56	48
50	8	7.01	50	100	43
60	15	7.76	12	71	4
62	40	7.91	20	65	1
67	8	7.53	25	100	14
71	16	7.49	38	38	100

[*] Probability of corrected chi-square or Fisher's exact 2 tailed test values.

fields had more than 1,000 rhizobia per gram of soil. In our study, nodulation of alfalfa completely failed in only one of the 85 soil samples (1%) and nodulation of sweetvetch in only 8 of the samples (9%). Rhizobia capable of infecting these two legumes apparently were present in both crop and noncropland throughout most of the geographic region represented by the soils sampled. This was quite different than the results reported by Mahler and Wollum (1982) in their investigation of the seasonal variation of *Rhizobium meliloti* in the more acidic soils of alfalfa hay and cultivated fields in North Carolina. In that state a major problem encountered with alfalfa establishment was described as due to the apparent lack of an effective indigenous soil *R. meliloti* population in fields without a previous alfalfa history.

Statistically significant differences ($P<0.05$) in frequency of nodulation of the two legumes were detected in 6 of the 27 soils associations tested (Table 2). Tests of homogeneity with probabilities of less than 5% were found for associations 1, 33, 45, 47, 60, and 62. In each instance the nodulation rate of alfalfa exceeded that of sweetvetch. The biological basis for the lack of homogeneity could not be positively related to cropping history, pH, soil association, or climax vegetation.

Alfalfa plants had more than twice as many, but significantly ($P<0.05$) smaller, nodules than sweetvetch plants (Table 3). Whenever the legumes were grown on soils of association 35, they had considerably more nodules than when grown on any of the other soil associations. Association 35 was represented by only one sample collected near Manila, Utah. The upland loam soil at that site supported growth of juniper trees (*Juniperus osteosperma*), big sagebrush (*Artemisia tridentata*), and a native legume (*Astragalus* sp.). The site also had a 10% slope to the south and was located at 1750 m elevation, but appeared very similar to a number of the other collection sites with soils that resulted in much lower numbers of nodules on both legumes.

Acetylene Reduction

Although the alfalfa plants had less shoot, root, and nodule biomass than sweetvetch plants, they exhibited approximately 30% higher acetylene reduction rates (Table 3). The difference was statistically significant ($P<0.05$). The overall mean for specific nodule activity for acetylene reduction as indicated by the amount of ethylene produced per hour per gram of nodule dry weight of alfalfa was more than six times higher than that for sweetvetch. The rate for alfalfa exceeded that for sweetvetch on 24 of the 27 soil associations. This supports previous observations by Johnson and Rumbaugh (1981) that acetylene reduction activity by alfalfa exceeded that of most other legumes grown in the intermountain area.

The relationships of acetylene reduction activity to shoot biomass of the two legumes when grown on each of the 27 soil associations were quite similar (Fig. 2). With few exceptions, sweetvetch was more responsive

TABLE 3. Means and ranges of plant weight and acetylene reduction, $N_2[C_2H_2]$, characteristics of legumes grown on soils representing 27 major soil associations of the northern Great Basin. The ranges are enclosed in parenthesis and are extremes of means for the 27 associations.

	Species	
Variable	*Hedysarum boreale*	*Medicago sativa*
Plant weight (mg)		
Shoot	81 (14–128)**	70 (20–101)**
Root	102 (12–172)**	83 (18–152)**
Nodules	2.9 (0.0–14.2)**	1.2 (0.0–3.8)*
Total	186 (26–284)**	159 (38–256)**
No. of nodules/plant	2.5 (0.0–40.8)**	5.8 (0.0–17.5)
Acetylene reduction activity		
Plant (μ moles/h)	0.06 (0.00–0.21)**	0.08 (0.00–0.26)*
Nodules (μ moles/h/g)	6 (0–22)*	38 (0–94)*

*,**Differences among means of the 27 associations within species were significant with $P<0.05$ and $P<0.01$, respectively.

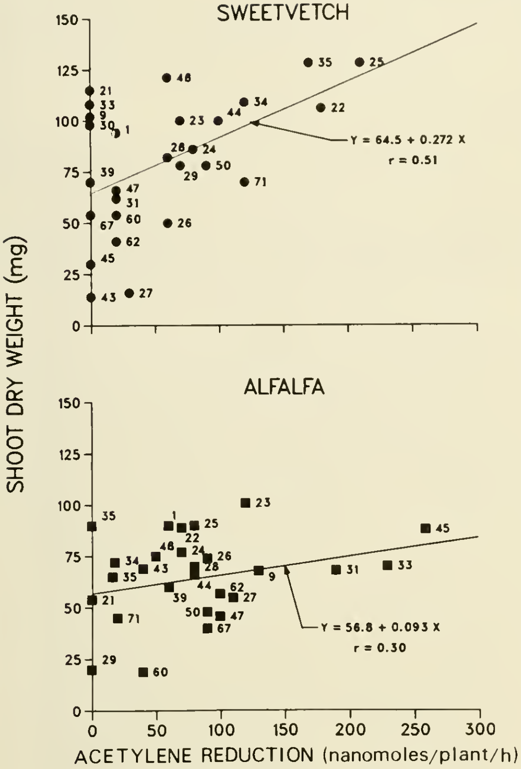

Fig. 2. Relationships of shoot weights to acetylene reduction activities of sweetvetch and alfalfa grown on soils of 27 major associations. See Table 1 for identification of the associations represented by the points and numbers.

than alfalfa to increased reduction, but the relative positions of points representing the associations were much alike. Exceptions could be detected. In an example of the exceptions, soil association 43, a group of aquic calciorthids and aquic ustifluvents, supported growth of alfalfa much better than growth of sweetvetch, although acetylene reduction was zero or low for both kinds of plants. Such differences may be related to differential nutritional demands or susceptibility to soilborne pathogens.

Stepwise forward multiple regression functions predicting whole plant and specific acetylene reduction activities explained about 25% of the observed variation in the dependent variables. Each function included 7 quantitative and 42 dichotomous independent variables. Activities of the two legume species were predicted with approximately equal precision. The presence or absence of wheat (*Triticum vulgare*) growing at the soil collection site was the single most important predictor of acetylene reduction by alfalfa. Similarly, the presence or absence of juniper trees was the single most important predictor of acetylene reduction by sweetvetch. It is highly probable that most wheat fields in northern Utah have been used to produce alfalfa at some time. Sweetvetch commonly occurs in association with juniper in natural stands. Although considerable redundancy in the information content of the independent variables used for prediction was anticipated, the magnitude of the multiple correlation coefficients was lower than expected, with values of 0.46 and 0.50 for whole plant and specific nodule activities, respectively, of alfalfa, and 0.48 and 0.46 for sweetvetch. Although complete nodulation failure with both legumes was observed with only one of the soil associations, nitrogen fixation rates (as indicated by acetylene reduction) could not be predicted very accurately. Also, the predictive functions for alfalfa were quite different than those for sweetvetch. Rank correlation coefficients for the order of entry of the independent variables into the regression equations for the two legumes were $r_s = -0.09$ and $r_s = 0.03$ for whole plant and specific nodule activities, respectively.

Conclusions

Almost all the major soil associations of northern Utah and presumably of the northern Great Basin contain indigenous rhizobia populations of appropriate types and numbers to nodulate *H. boreale* and *M. sativa*. Nitrogen fixation (acetylene reduction activity) by these legumes varied significantly ($P < 0.05$) when grown in the different soils with their respective indigenous rhizobia. These activity levels could not be accurately predicted using any combination of the 49 climatic, edaphic, and vegetation variables included in this study.

Literature Cited

Barber, L. E. 1980. Enumeration, effectiveness, and pH resistance of *Rhizobium meliloti* populations in Oregon soils. Soil Sci. Soc. Amer. J. 44:537–539.

Hely, F. W., and J. Brockwell. 1962. An exploratory survey of the ecology of *Rhizobium meliloti* in inland New South Wales and Queensland. Aust. J. Agric. Res. 13:864–879.

Jing, Y., A. S. Paau, and W. J. Brill. 1982. Leghemoglobins from alfalfa (*Medicago sativa* L. Vernal) root nodules. I. Purification and in vitro synthesis of five leghemoglobin components. Plant Sci. Letters 25:119–132.

Johnson, D. A., and M. D. Rumbaugh. 1981. Nodulation and acetylene reduction by certain rangeland and legume species under field conditions. J. Range Manage. 34:178–181.

Katznelson, H. 1940. Survival of microorganisms introduced into soil. Soil Sci. 49:283–293.

Lorenz, R. J. 1982. Alfalfa in western grazing management systems. Pages 1–3 *in* A. C. Wilton, ed., Alfalfa for dryland grazing. Agric. Info. Bull. No. 444, USDA. U.S. Government Printing Office, Washington, D.C.

Mahler, R. L., and A. G. Wollum, II. 1982. Seasonal variation of *Rhizobium meliloti* in alfalfa hay and cultivated fields in North Carolina. Agron. J. 74:428–431.

Nichols, J. T., and J. R. Johnson. 1969. Range productivity as influenced by biennial sweetclover in western South Dakota. J. Range Manage. 22:342–347.

Nutman, P. S., and G. J. S. Ross. 1970. *Rhizobium* in the soils of the Rothamsted and Woburn farm. Rothamsted Exp. Sta. Rept. 1969. Part 2, p. 148.

Rice, W. A., D. C. Penney, and M. Nyborg. 1977. Effects of soil acidity on rhizobia numbers, nodulation, and nitrogen fixation by alfalfa and red clover. Canadian J. Soil Sci. 57:197–203.

Rumbaugh, M. D. 1982. Reseeding by eight alfalfa populations in a semiarid pasture. J. Range Manage. 35:84–86.

Rumbaugh, M. D., D. A. Johnson, and G. A. Van Epps. 1982. Forage yield and quality in a Great Basin shrub, grass, and legume pasture experiment. J. Range Manage. 35:604–609.

Sagardoy, M. A. 1981. Number and distribution of *Rhizobium meliloti* and other microbial populations in soils. Anales de Edafologia y Agrobiologia 40:889–895.

Van Rensburg, H. J., and B. W. Strijdom. 1982. Competitive abilities of *Rhizobium meliloti* strains considered to have potential as inoculants. Applied and Environmental Microbiology 44:98–106.

Waksman, S. A., and H. B. Woodruff. 1940. Survival of bacteria added to soil and the resultant modification of soil population. Soil Sci. 50:421–427.

Wilson, L., M. E. Olsen, T. B. Hutchings, A. R. Southard, and A. J. Erickson. 1975. Soils of Utah. Utah Agric. Exp. Sta. Bull. 492:1–94.

Appendix

Scientific names of the plant species listed in Table 1 are the following: Antelope bitterbrush (*Purshia tridentata* [Pursh] DC.), Basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Love), Bearded wheatgrass (*Elymus subsecundus* [Link] A. & D. Love), Big sagebrush (*Artemisia tridentata* Nutt.), Bigtooth maple (*Acer grandidentatum* Nutt.), Birchleaf mountain mahogany (*Cercocarpus betuloides* Nutt.), Black sagebrush (*Artemisia nova* A. Nels.), Blue wildrye (*Elymus glaucus* Buckl.), Bluebunch wheatgrass (*Elytrigia spicata* [Pursh] D. R. Dewey), Bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), Curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.), Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco), Gambel oak (*Quercus gambelii* Nutt.), Greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), Greenleaf manzanita (*Arctostaphylos patula* Greene), Indian ricegrass (*Oryzopsis hymenoides* [Roem. & Schult.] Ricker), Mountain brome (*Bromus marginatus* Nees ex Steud.), Needle and thread (*Stipa comata* Trin. & Rupr.), Nuttall saltbush (*Atriplex nuttallii* H. & C.), Pinyon pine (*Pinus edulis* Engelm.), Quaking aspen (*Populus tremuloides* Michx.), Sedges (*Carex* spp.), Shadscale (*Atriplex confertifolia* [Torr. & Frem.] S. Wats.), Slender wheatgrass (*Elymus trachycaulus* [Link] Gould ex Shinners), Tufted hairgrass (*Deschampsia caespitosa* [L.] Beauv.), Utah juniper (*Juniperus osteosperma* [Torr.] Little), Western wheatgrass (*Pascopyrum smithii* [Rydb.] Love), and Winterfat (*Ceratoides lanata* [Pursh] J. T. Howell).

CHECKLIST OF TIGER BEETLES FROM IDAHO (COLEOPTERA: CICINDELIDAE)

Gary A. Shook[1]

Abstract.— Sixteen species of Tiger Beetles are listed for Idaho, along with the counties of occurrence for each species. Three species are placed in a checklist of Idaho species for the first time: *Cicindela depressula depressula* Casey, *Cicindela parowana wallisi* Calder, and *Cicindela decemnotata decemnotata* Say.

Leng (1920) listed 5 species of Tiger Beetle from Idaho. Hatch (153:340) treated 10 species, to which Rumpp (1967) added 3 more species. The most recent checklist included only those 13 Idaho species (Boyd 1982:31). Three other species, *Cicindela depressula depressula* Casey, *Cicindela parowana wallisi* Calder and *Cicindela decemnotata decemnotata* Say, were known to occur, but did not appear in reviewed literature. The following checklist includes those omitted species and presents additional distribution for Idaho species. The list is offered in anticipation of a more extensive monograph of Idaho Tiger Beetles.

Idaho has 44 counties. Those counties of occurrence accompany each species. The use of subspecific names is avoided if, at this time, the subspecific status is questioned or under review. The list includes the following.

Cicindela (Cicindela) *longilabris* Say: Boise, Bonner, Boundary, Clearwater, Idaho, Latah.

Cicindela (Cicindela) *nebraskana* Casey: Caribou, Cassia, Franklin, Fremont, Lemhi, Twin Falls.

Cicindela (Cicindela) *oregona oregona* LeConte: Ada, Adams, Bannock, Bear Lake, Benewah, Blaine, Boise, Bonner, Bonneville, Boundary, Camas, Canyon, Cassia, Clearwater, Elmore, Franklin, Fremont, Gem, Gooding, Idaho, Kootenai, Latah, Lewis, Minidoka, Nez Perce, Owyhee, Payette, Power, Shoshone, Twin Falls, Valley, Washington. Note: Freitag (1965) listed a hybrid *C. o. oregona* x *gutifera* from Bannock, Bear Lake, Franklin, Fremont, and Lemhi counties.

Cicindela (Cicindela) *repanda repanda* Dejean: Ada, Bear Lake, Boise, Clearwater, Idaho, Latah, Lewis, Nez Perce, Owyhee, Shoshone, Twin Falls, Washington.

Cicindela (Cicindela) *depressula depressula* Casey: Idaho County.

Cicindela (Cicindela) *hirticollis hirticollis* Say: Fremont, Idaho, Lewis, Nez Perce, Washington.

Cicindela (Cicindela) *arenicola* Rumpp: Fremont, Minidoka, Owyhee.

Cicindela (Cicindela) *columbica columbica* Hatch: Idaho, Lewis.

Cicindela (Cicindela) *purpurea auduboni* Olivier: Ada, Blaine, Boise, Elmore, Gem, Latah, Lincoln, Minidoka, Nez Perce, Oneida, Owyhee, Twin Falls.

Cicindela (Cicindela) *plutonica* Casey: Ada, Canyon, Cassia, Elmore, Lemhi, Owyhee.

Cicindela (Cicindela) *parowana wallisi* Calder: Elmore, Gem, Owyhee.

Cicindela (Cicindela) *decemnotata decemnotata* Say: Bannock, Bear Lake, Bingham, Butte, Cassia, Lincoln, Oneida, Twin Falls.

Cicindela (Cicindela) *tranquebarica* Herbst: Ada, Bannock, Benewah, Blaine, Boise, Bonner, Gooding, Idaho, Kootenai, Latah, Lewis, Lincoln, Minidoka, Owyhee, Power, Teton, Twin Falls, Valley.

Cicindela (Cicindelidia) *haemorhagica haemorhagica* LeConte: Ada, Adams, Boise, Canyon, Cassia, Elmore, Franklin, Gooding, Jerome, Minidoka, Owyhee, Power, Twin Falls, Washington.

Cicindela (Cicindelidia) *willistoni echo* Casey: Elmore, Owyhee.

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Cicindela (Cylindera) *terricola imperfecta* LeConte: Bear Lake, Canyon, Caribou, Cassia, Custer, Jerome, Gooding, Twin Falls.

Locality data were taken from specimens in the following collections: Boise State University (Charles Baker), California Academy of Sciences (David Kavanaugh), Don Brothers, College of Idaho (William Clark), Idaho State University (Robert Anderson), Norman Rumpp, University of Idaho (William Barr), Utah State University (Wilford Hansen), and my collection.

All specimen identifications were made or verified by myself or by Mr. Norman Rumpp.

Thanks to all those who permitted this review of their material, with a special thanks to Norman Rumpp for his comments regarding this checklist.

Literature Cited

Boyd, H. 1982. Checklist of Cicindelidae: The tiger beetles. Plexus Publishing, New Jersey.

Freitag, R. 1965. A revision of the North American species of the *Cicindela maritima* group with a study of hybridization between *Cicindela duodecimguttata* and *oregona*. Questiones entomologicae 1965:87–170.

Hatch, M. H. 1953. Beetles of the Pacific Northwest. Univ. of Washington Press, Seattle. Vol. 1.

Leng, C. W. 1920. Catalogue of the Coleoptera of America North of Mexico. Sherman, New York.

Rumpp, N. 1967. A new species of *Cicindela* from Idaho (Coleoptera: Cicindelidae). Proceedings of the California Academy of Sciences (4)35(7):129–140.

EMERGENCE OF ADULT PANDORA MOTHS IN ARIZONA

J. M. Schmid[1]

ABSTRACT.— Adult pandora moths began emerging in late July, and peak daily emergence occurred during 10–15 August. The mean density of moths emerging per 929 cm^2 of ground surface ranged from 0.1 to 2.4. The ratio of emerging males to females varied from 3–4:1 during the initial days of emergence to 1:1.5 during the last 10 days of August. Postemergence behavior is described and discussed in relation to egg mass deposition and species survival.

Prior to the current pandora moth, *Coloradia pandora* Blake (Lepidoptera: Saturniidae), infestation on the Kaibab National Forest surrounding Jacob Lake, Arizona, life history information on this insect was derived from the works of Patterson (1929), Massey (1940), and Wygant (1941) on populations in California and Colorado, respectively. Near Jacob Lake in 1980, adults emerged much later than previously recorded. Similarly, other aspects of the pandora moth's life history did not coincide with previous reports. This study was conducted to determine the emergence period of adults and their subsequent behavior.

Study Area and Methods

A general description of the infested area is presented in Schmid et al. (1982b). Four locations were selected within this general area and were assigned plot numbers corresponding to adjacent Forest Service roads or U.S. Highway 89A (Fig. 1). These locations were selected because of abundant pupae, substantial elevational gradients, and different aspects (Table 1).

On each plot, screen cages were placed on the surface of the ground to catch emerging adults. The cages on Forest Service Road 246, Forest Service Road 482, and U.S. Highway 89 plots were placed at three different elevations within each plot, representing (1) flat ridge top, (2) ravine bottom, and (3) midslope—approximately halfway between the ridge top and the ravine bottom (Table 1). Within each elevational position, cages were placed 5 m apart either in a straight line or along the contour.

Cages on the Forest Service Road 257 plot were established to monitor the effects of prescribed burning on pupal mortality. They were on a relatively flat area with insignificant elevational and aspectual influences. The cages were laid out in a north-south pattern with the cages at 20 m intervals, on parallel N-S lines that were 10 m apart.

Cages were installed 21–22 July 1982 and were checked daily thereafter until 30 August 1982. Cage examination began each day at 0600 local time. After adults began emerging, the cages were checked in the morning at the usual time and again just before dark to determine if adults were emerging only during daylight or throughout the entire day. The number of males and females emerging in each cage was recorded daily to determine the sex ratio. The mean number of adults emerging per 929 cm^2 was computed for each elevation on each plot, and the means were compared with a one-factor analysis of variance to determine significant differences among elevational positions, $\alpha = 0.05$.

To determine adult longevity, 12 adults were collected as they emerged on 31 July 1982, were separated according to sex, and were placed in holding cages. The cages were checked daily thereafter until all adults were dead. On 5 August 1982, another 10 females were collected, were placed in cages, and were observed daily until they died.

Various amounts of time were spent each day during the first half of the emergence

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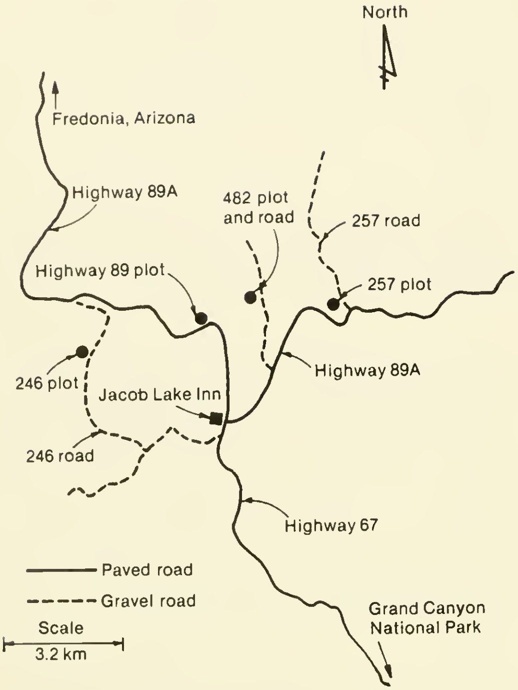

Fig. 1. Geographical location of study areas.

period observing adult behavior as they emerged from the ground. Individual adults were observed for 1–2 hours following emergence. Sex ratios of emerged adults clinging to mature tree boles were determined in the evening.

Results and Discussion

Emergence period.— Adults began emerging on the plots 28 July 1982. A few adults were observed near lights at Jacob Lake a few days earlier, but their numbers were similar to what emerged in the cages. The daily number of emerging adults continued at a low level until 4 August, when the number increased substantially (Fig. 2). Numbers generally increased thereafter, and maximum numbers of adults emerged during 10–15 August. After mid-August, numbers decreased until 30 August, when daily emergence averaged 1–2 adults per day. Adults were observed on 22 September, after the checking of cages had long since ceased, indicating that adults continued to emerge well after most of the population emerged.

Although these data accurately reflect the general emergence pattern, it does not reflect the total number of emerging moths. If an adult emerged for every 929 cm^2 of ground (approximately weighted average from Table 2), then more than 100,000 adults emerged from each infested hectare. If this density is assumed for the approximately 8000 hectares moderately to severely defoliated by the previous larval generation, then approximately 800 million moths have flown during the emergence period. Although this figure is based on limited emergence data and an approximation for total infested area and, thus, may be considered speculative, the numbers observed around the lights at Jacob Lake, around the bases of trees, and flying in the woods suggest otherwise.

Adults emerged at the lower-elevation Forest Service Road 257 plot about 10 days before the first emerging adults on the U.S. Highway 89A plot. The combination of higher elevation and north aspect probably caused slower development on the U.S. Highway 89A plot.

Moths emerged after late summer rains began on the North Kaibab. Rains soften the dry, cementlike soil surface and allow the adult to emerge with less difficulty and consequent increased population survival.

Density of emerging adults.— The number of adults emerging per 929 cm^2 ranged from 0 to 13 (Table 2). Mean densities on ridge tops and midslopes were generally higher than in ravines, but a significant difference between ridge top and ravine was

Table 1. Characteristics of the four emergence plots.

Plot	Aspect	Elevational range	Number of cages/ plot	Number of cages/ elevational position	Cage size
Forest Service Road 246	East	2348–2378 m	51	17	1858 cm^2
U.S. Highway 89A	North	2363–2386 m	51	17	1858 cm^2
Forest Service Road 482	West	2317–2348 m	48	16	1858 cm^2
Forest Service Road 257	None	2325 m	100	100	929 cm^2

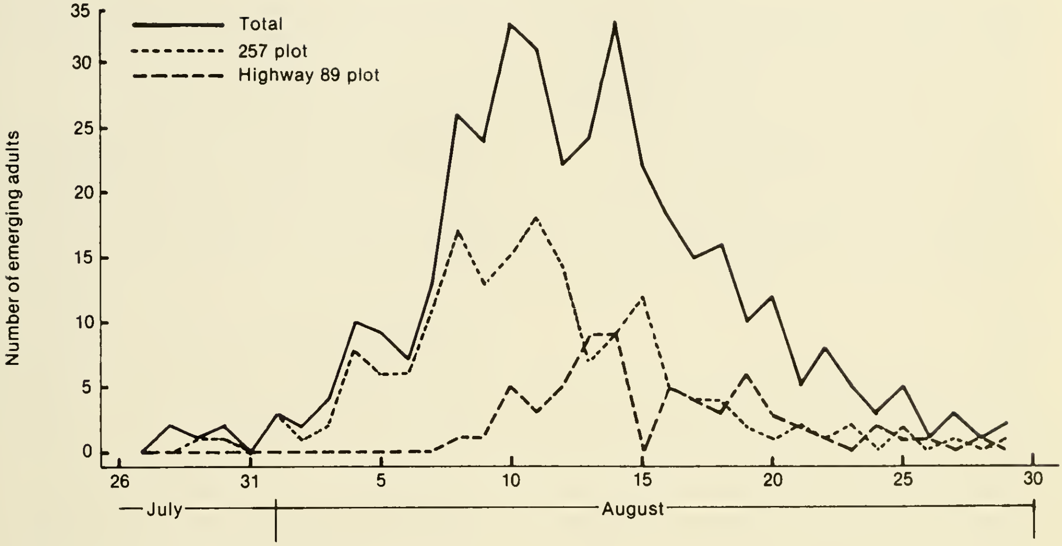

Fig. 2. Daily emergence of pandora moths, 1982.

found only on the 482 plot (Table 2). The low densities in ravine bottoms were expected, because previous observations indicated defoliation was less on trees there. The reason for this elevational variability is not known, but because females are generally active only at night, and the ravine bottoms are noticeably cooler, females may be most active in the warmer thermoclines on the ridge tops and less active in the ravine bottoms. This explanation may also account for the broader pattern of infestation, wherein successive ridges had greater densities of larvae and greater defoliation than did broad, lower elevation areas between them.

Sex ratio.— Both sexes emerged during the first 10 days of the emergence period, but males outnumbered females by a 3–4:1 margin. As the emergence period progressed, the sex ratio shifted so it was essentially 1:1 during peak emergence and then 1:1.5 during the last 10 days that emergence was monitored.

Behavior.— Adults crawled upward through the soil and litter from their pupal site, so the first evidence of their emergence was movement of the litter. After emerging, they crawled over the litter surface until they encountered any upward oriented object, including tree boles, dead limbs, grass stems, *Solidago* sp., *Lupinus* sp., cones, and stumps. All were climbed when encountered, but most of the herbaceous plants failed to support the adult. When the stems broke or

Table 2. Number of emerging pandora moth adults per 929 cm^2.

Site	Forest Service Road 246 plot	U.S. Highway 89A plot	Forest Service Road 482 plot	Forest Service Road 257 plot
		$\bar{x} \pm$ S.D.		
Ridge top	.4 ± .8 a[1]	.8 ± 1.2 a	2.4 ± 3.2a	1.7 ± 2.4
Midslope	.6 ± 1.1 a	.8 ± 1.1 a	0.4 ± 0.8a b	NA
Ravine bottom	.1 ± .2 a	.2 ± 0.4 a	0.2 ± 0.4b	NA
		Range		
Ridge top	0–3.0	0–4.0	0–12.5	0–13
Midslope	0–3.5	0–4.5	0– 2.5	NA
Ravine bottom	0–0.5	0–1.5	0– 1.5	NA

NA = Not applicable

[1] Within a particular location, means followed by the same letter are not significantly different, $\alpha = .05$.

bent, sending the adult to the ground, the adult resumed crawling and either repeated this process with other herbaceous stems or finally encountered a wooden object. Ninety-nine percent of the time adults settled on the boles of all sizes of ponderosa pine.

Adults sought upward-oriented objects to find a place to hang and expand their wings. The wings are not fully formed when they emerge, and the wings begin to expand once the adults settle on an upward-oriented object.

Most adults settled on the tree boles from within a few centimeters to 2 m above ground, with maximum ascension being influenced by tree size and perhaps the distance the adult crawled over the ground surface before reaching the tree. On seedlings and saplings, adults climbed to various heights, and frequently climbed as high as they could go. On larger trees, adults settled various distances aboveground ranging from a few centimeters to over 6 m in a few cases. Some adults that crawled for 10–20 m before encountering a tree settled within 1 m of the ground, and others that crawled lesser horizontal distances settled higher on the bole.

Adults appeared to discern large trees when they were within 2 m of them, but seemed to encounter seedlings and saplings by chance. Adults frequently crawled past seedlings and saplings that could have provided suitable resting places and continued crawling until encountering another object. Large trees were not bypassed when the adult was within 2 m of them, but adults frequently did not crawl to large trees that were closest to their emergence hole when the distance to the closest tree was more than 2 m.

Adults usually settled in a shaded spot on the tree where they could hang without the abdomen touching any surface. They settled into this position with a lateral rocking motion, during which the antennae were folded close to their ventrolateral surface just above the legs. The wings were expanded within 15 minutes. At first, the leading edge of the unexpanded wings were oriented laterally from the body. As they expanded, the leading edges came together over the dorsal surface of the abdomen and projected outward from the body. The wings remained in this position for another 30 to 45 minutes. Then the leading edges were brought to the lateral sides of the abdomen and the trailing edges formed a triangular tent over the abdomen.

Adults usually remained in the same positions on the boles for the remaining daylight hours unless disturbed or unless their location became exposed to direct sunlight. In such cases, the disturbed adults frequently moved higher on the tree. On sunny days, adults emerging in the morning were usually found on the north and west sides of the trees. Adults emerging in the afternoon were found on the north and east sides of the trees. On cloudy days, more adults were seen on southern exposures.

During the first days of the emergence period, little flight and mating activity was observed. Few females mated during the wing expansion period, and no egg masses were observed on tree boles. As the emergence period progressed, more mature adults were present, and hundreds of males were observed flying during the daylight hours. Males frequently hovered 8–15 cm away from the boles and flew vertically or laterally around the circumference at this distance, apparently in search of females. Newly emerged females frequently mated as soon as they began crawling up the tree or while at rest during wing expansion. As a result, egg masses became abundant in the first 1–2 meters of the bole. This probably accounts for the greater density of egg masses in the first 30 cm of the bole as observed by Schmid et al. (1982a). Furthermore, the highly disproportionate sex ratio favoring males in the initial days of emergence decreases the possibility that females go unmated. This apparently increases the chances of survival of the species.

Females generally were not observed flying during daylight hours. This observation, the tendency to avoid direct sunlight and the tremendous nighttime activity around lights at Jacob Lake, indicates most adults, particularly females, are active at night. Males nearing death were the adults most active during daylight hours.

Longevity.— All but one caged adult died within one week after emergence. The cages kept them relatively inactive so their life spans may have been artificially shortened.

However, seven days is probably the life span of the adult in the forest.

LITERATURE CITED

MASSEY, C. L. 1940. The pandora moth (*Coloradia pandora* Blake). A defoliator of lodgepole pine in Colorado. Unpublished thesis. Duke Univ., Durham, North Carolina. 33 pp.

PATTERSON, J. E. 1929. The pandora moth, a periodic pest of western pine forests. U.S. Dept. Agric. Tech. Bull. 137. 20 pp.

SCHMID, J. M., P. A. FARRAR, AND J. C. MITCHELL. 1982a. Distribution of pandora moth egg masses and pupae near Jacob Lake, Arizona. Environ. Entom. 11:701–704.

SCHMID, J. M., D. BENNETT, R. W. YOUNG, S. MATA, M. ANDREWS, AND J. MITCHELL. 1982b. Sampling larval populations of the pandora moth. USDA Forest Service Research Note RM-421. 5 pp.

WYGANT, N. D. 1941. An infestation of the pandora moth, *Coloradia pandora* Blake, in lodgepole pine in Colorado. J. Econ. Entomol. 34:607–702.

MULTIPLE ECTOPIC LIMBS IN A WILD POPULATION OF *HYLA REGILLA*

Timothy D. Reynolds[1] and Trent D. Stephens[2]

Abstract.— A wild population of Pacific tree frogs (*Hyla regilla*) in Idaho exhibited a high incidence (22%) of hind limb abnormalities. This situation is discussed with reference to similar occurrences reported for isolated populations of the species in the Pacific Northwest.

Isolated cases of amphibians found in nature with extra legs (polymelia) are not uncommon (Van Valen 1974). Occurrences of significant numbers of such defects among small populations of amphibians, however, are less common and of much greater importance. Reports of polymelic populations (Van Valen 1974) have occurred fairly regularly since 1948 and have included *Hyla regilla*, *Ceptodactylus* sp., *Rana catesbeiana* (two separate populations), *Rana esculenta ridibunda*, and "frogs." These reports have come from a wide geographical range including Russia, Ecuador, and several sites in the United States (Montana, New Jersey, Ohio, and Mississippi).

One report not included in the Van Valen (1974) review concerns a second population of polymelic *Hyla regilla* in a small pond in Spokane, Washington (Miller 1968). We will expand upon the report of polymelia in *Hyla regilla* that was included in the Van Valen review (1974). In August 1958 (the same year as polymelic *Rana catesbeiana* were discovered in Mississippi, Volpe 1981:3–4) several polymelic *Hyla regilla* were taken from a pond near Polson, Montana (14 malformed of a total population of 73 examined; Hebard and Brunson 1962). The next year four more malformed specimens were taken from the same Montana pond (of a total of 13 examined), and in 1960 and 1961 similar proportions of polymelia were observed there. The report of the Spokane population (Miller 1968) was very brief and had few details. That population was sampled only once.

The purpose of the present paper is to report a third population of polymelic *Hyla regilla* found in the fall of 1981 in Boise, Idaho. We will discuss the striking regionality of this defect and its implications concerning etiology.

Study Area

Our specimens were collected from a small (approximately 0.2 ha) pond located in a low-lying area within a housing complex on the southwest side of Boise, Ada County, Idaho (SW ¼ SW ¼ Sec. 2, T2N, R1E Boise Meridian; Universal Transverse Mercator Coordinates 482000 N, 555650 E, Zone 11). Maximum water depth was 0.5 m. Cattail (*Typha latifolia* L.) was the dominant vegetation of the pond environs. There was no obvious water inlet or outlet for the pond. The Paris lateral canal, part of the local irrigation network, passed within 10 m of the north side of the pond. Presumably, underground seepage from the canal was the source of pond water. A local resident stated that the pond was often dry or nearly so in the early spring, but would increase in size by late summer to nearly one acre (0.4 ha). For mosquito control purposes, the Ada County Mosquito Abatement District applied Bx-2 coated granules to the pond at a dosage rate of 5 pounds per acre on 26 May, 16 and 31 June, and 31 July 1981 (R. Shore, pers. comm.). Bx-2 granules contain 2% (by weight) of the larvicide Baytex (FMC Corporation). This compound has no known teratological effects, but is reported to be toxic to a variety of invertebrate and vertebrate classes.

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Methods

Abnormal frogs in the pond were noticed by a local resident and reported to the pesticide inspector of the Idaho Department of Agriculture ca 5 September 1981. One of us (TDR) was contacted and collecting trips were made to the pond on 10, 16, and 23 September and 3 October 1981. Using long-handled aquatic insect nets, efforts were made to capture all frogs observed. The majority of the frogs captured were transported to the biology departments of Boise State and Idaho State universities and placed in aquaria for future breeding and teratological experiments. Some normal individuals were returned to the pond after close inspection revealed no limb anomalies.

Results

A total of 54 Pacific tree frogs (*Hyla regilla*) were captured. Thirteen (22%) exhibited hind limb abnormalities. No fore limb anomalies were noted. The defects ranged from a small midcaudal bleb or polydactyly of one foot to complete and multiple hind limb polymelia with concomitant polydactyly (Table 1; Figs. 1 and 2). Abnormalities occurred in equal numbers on the left and right sides of the animals. The degree of function of the polymelic limbs was variable, and ranged from no discernible function in some ectopic limbs to nearly normal function in others.

Table 1. Occurrence, sidedness, and severity of hind limb abnormalities in a wild population of *Hyla regilla* from Boise, Ada County, Idaho, 1981.

Hind limb morphology	Number of individuals affected			
Normal	41			
Abnormal	*Left side*	*Mid-line*	*Right side*	*Total*
Midcaudal blebs	0	2	0	2
Clinodactyla	1	0	0	1
Polydactyla	2	0	1	3
Partial polymelia	2	0	0	2
Partial polymelia and polydactyla	0	0	1	1
Complete polymelia and polydactyla	0	1	1	2
Multiple complete polymelia and polydactyla	0	0	2	2
Totals	5	3	5	13

Discussion

Although the sample size in this study was small, the results indicate a high incidence (22%) polymelia and polydactyly in a wild hylid population. The polymelia observed in this study involved only the hind limbs. This is consistent with Van Valen's (1974) statement that the fore limbs are rarely affected in polymelic populations. This Idaho population of hylids exhibited the same types of defects as the polymelic hylids found in Montana and Washington. This is consistent with Van Valen's (1974) observation that "specific kinds of abnormalities are different for each species or subspecies (but not between populations within species)."

All three reported cases of polymelic populations of *Hyla* have occurred in the intermountain regions of the Northwest United States (i.e., Montana, Washington, and Idaho). If polymelia was ubiquitous to the entire population of *Hyla regilla*, it would be

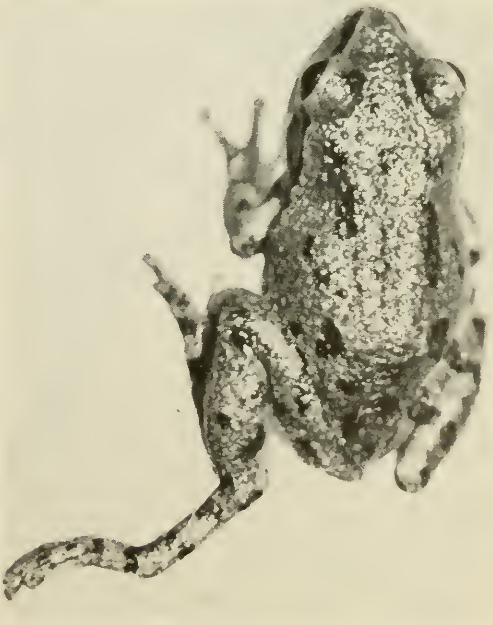

Fig. 1. Live *Hyla regilla* taken from the north edge of the Boise pond, 3 October 1981. The ectopic leg represents a duplication of the entire leg distal to the knee.

much more likely for such malformations to be noted in the Pacific coast populations, where both frogs and observers are more common, than in the more remote reaches of the hylid range. Indeed, the three abnormal populations were confined to isolated pockets of *Hyla regilla* located well outside the main geographic distribution of the species (Fig. 3).

It is conceivable that these three populations of *Hyla* represent only marginally successful isolates and that whatever environmental factors restrict the existence of *Hyla* in adjacent, nonpopulated areas contribute to the malformations in the isolates. A large number of environmental factors could be postulated. The most obvious restricting factor in that general region of the United States is climate. The three sites where the hylid populations exist are areas of comparatively greater rainfall and more moderate temperatures than the general, more hostile environment of that region.

Van Valen (1974) discussed possible etiologies in his review of polymelia. They included genetic defects, viruses, parasites, radiation, pH, temperature, and desiccation. Of that list, the last two are the most interesting in relation to the isolated *Hyla* populations being discussed. The pond in Boise is reported as being dry for a large portion of the year. One of us (TDS) visited the pond in May 1982 and found the pond completely dry. It is thus possible that the *Hyla* of that pond are breeding later than normal or that the eggs are laid in rather dry conditions. Voitkevich (1958, 1961) noted that the polymelous *Rana esculenta ridibunda* that he observed in one reservoir were found mostly in the region of cold spring water. He suggested that cold-related developmental retardation may result in such malformations. Lastly, Miller (1968) noted that the pond where the

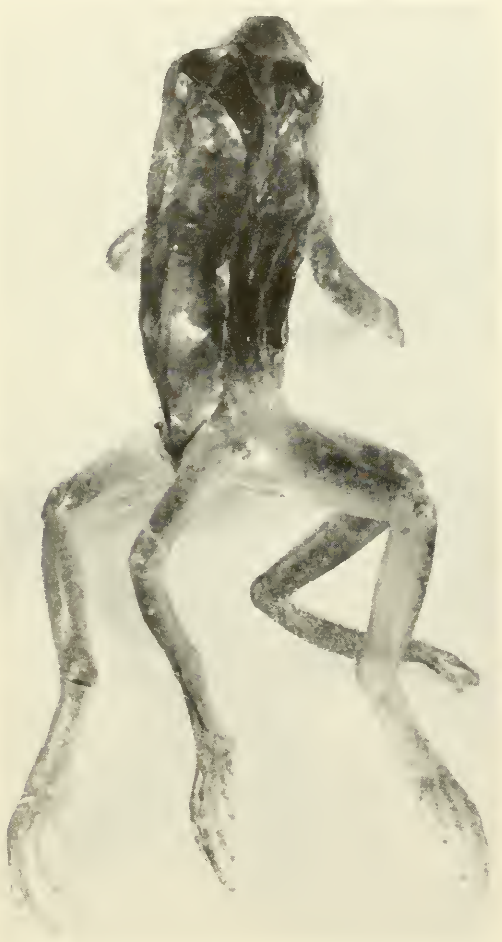

Fig. 2. Fixed *Hyla regilla* taken from the north edge of the Boise pond, 3 October 1981. The frog exhibits four complete legs joined at the pelvic girdle. It is difficult to determine which legs are "normal" and which are "abnormal."

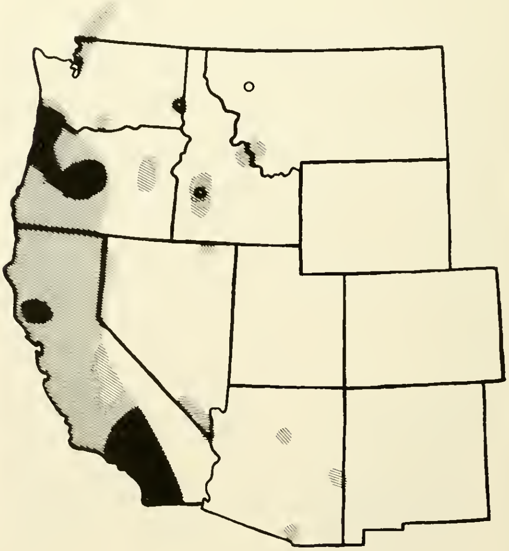

Fig. 3. Outline map of the western United States, with the distribution of *Hyla regilla* indicated by diagonal lines. High concentration areas are marked by crosshatching. The locations of the three polymelic *Hyla* populations are indicated by the circles (After Jameson et al. 1966; Fig. 13).

Washington *Hyla* were collected had been sprayed for mosquitoes. The Idaho pond had also been sprayed for mosquitoes. Nevertheless, such observations cannot be considered as anything more than coincident at this point.

We hope to follow up on all three Northwestern *Hyla* populations in the future in an attempt to gather more information about possible etiology.

LITERATURE CITED

HEBARD, W. B., AND R. B. BRUNSON. 1963. Hind limb anomalies of a Western Montana population of the Pacific tree frog, *Hyla regilla* Baird and Girard. Copeia 1963:570–572.

JAMESON, D. L., J. P. MACKEY, AND R. C. RICHMOND. 1966. The systematics of the Pacific tree frog, *Hyla regilla*. Proc. California Acad. Sci. 33:551–620.

MILLER, C. E. 1968. Frogs with five legs. Carolina Tips 31.

VAN VALEN, L. 1974. A natural model for the origin of some higher taxa. J. Herpetol. 8:109–121.

VOLPE, E. P. 1981. "Understanding Evolution." Wm. C. Brown Co., Dubuque, Iowa.

VOITKEVICH, A. A. 1958. A peculiar reduction of the shin-bone in the doubling of the limb in the frog in nature. Doklady Akad. Nauk SSSR 128:28–31.

______. 1961. Le developpement des extremities surnumeraires chez les amphibiens. Bull. Biol. France Belgique 95:569–600.

PLAGUE IN PINE MARTENS
AND THE FLEAS ASSOCIATED WITH ITS OCCURRENCE

W. J. Zielinski[1]

Abstract.— Thirteen pine martens (*Martes americana*) were sampled periodically from July 1979 to September 1980 for plague (*Yersinia pestis*) antibodies and their fleas collected and identified. Four individuals were positive for plague antibodies on 8 of 24 sampling occasions. Titer peaks in these individuals occurred simultaneously in early winter but fell to undetectable levels by late spring. A chipmunk flea (*Monopsyllus ciliatus*) was the most common ectoparasite constituting 55% of all individuals collected. Thirty-one percent of all fleas belonged to *Chaetopsylla floridensis*, a species previously unreported in California. The remains of ground-dwelling sciurids (chipmunks, *Eutamias* spp., and ground squirrels, *Spermophilus* spp.) were very common in marten scats during the period preceding elevated titers. For this reason, and the fact that 92% of all fleas collected from martens during this same period were found more commonly on chipmunks and ground squirrels, these rodents were implicated as the source of the martens' exposure to plague.

Plague is an infectious zoonotic disease found primarily in wild rodents in the western United States. Fleas serve as the vector of the disease agent. Carnivores are infected secondarily while feeding upon moribund and dead infected animals (Rust et al. 1971) or from contact with fleas residing in rodent burrows or nests (Eads et al. 1979). Because most carnivores appear to develop only transient clinical signs to plague (Marchette et al. 1962, see Rust et al. 1971, for feline exceptions) and have larger home ranges than rodents, they play an important role in transferring infected fleas to uninfected rodent populations (Eads et al. 1979). Rodent predators also serve as sentinel species for monitoring plague (Poland and Barnes 1979, Messick et al. 1983). Despite their importance, the contribution of rodent predators to the epidemiology of plague is poorly known (Messick et al. 1983). In California, the pine marten feeds primarily on the rodents that are confirmed plague host reservoirs. Plague has been detected in martens elsewhere (Barnes 1982), but little information was available regarding the ecology of the marten population at the site. Presented here are the first records of plague in California pine martens, the flea fauna discovered, and information on marten diets and home ranges.

Materials and Methods

Field work was concentrated in the 40 km^2 Sagehen Creek drainage, located on the eastern side of the Sierra Nevada in Nevada County, California. This area is classified as having "intermediate potential" for epizootic plague (Murray 1964), and evidence of decimation of ground squirrel populations has been documented at nearby Tahoe City (Murray 1971). Thirteen pine martens were captured at least once each from July 1979 to September 1980 and were immobilized with a combined intramuscular injection of ketamine-hydrochloride (Vetalar, 100 mg/ml, Parke-Davis, Detroit, MI) and acetylpromazine maleate (Acepromazine, 10 mg/ml Ayerst Laboratories, Inc., New York, N.Y.). During initial captures, and at several recaptures for those animals trapped often, a toenail was cut to the quick and blood was collected on a paper strip (Wolff and Hudson 1974). These samples were sent to the Plague Branch, Centers for Disease Control, Fort Collins, Colorado, for serological testing. Development of antibody gives evidence of prior infection with plague. Results are reported as a dilution ratio of 1:32 to 1:16,384 with titers ≥1:32 considered positive. Fleas were

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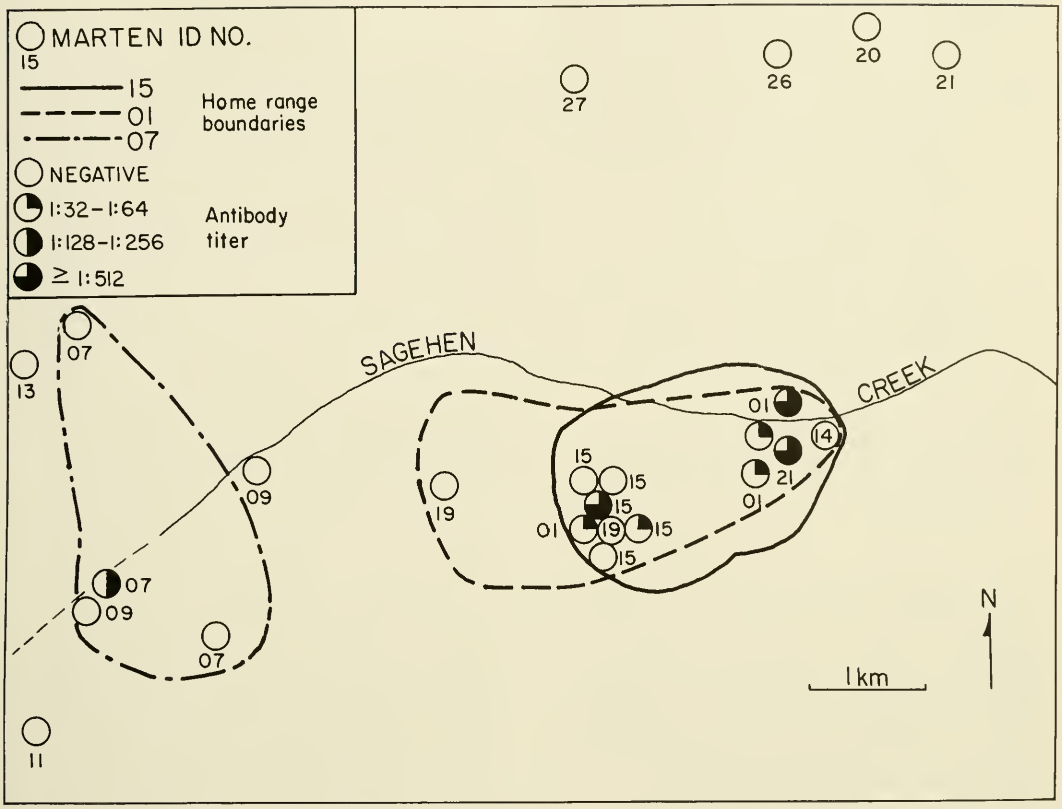

Fig. 1. Marten plague titers and spatial distribution of captures at which a blood sample was collected (Home range boundaries are included for three animals, and each represents the outermost points of 25 to 300 locations).

discovered by close examination of the marten's pelage after brisk brushing and were preserved in 70% ethanol.

Home range information was obtained by monitoring the location of 6 martens fitted with radio-transmitter collars (SB2, AVM Instrument Co., Champagne, IL 61820). Martens were located by approaching the signal on foot with a small hand-held antenna and receiver. Spencer (1981) analyzed the characteristics of marten home ranges in detail, but for purposes of this paper the home range perimeters are defined by the outermost radio locations.

Marten food habits were studied by analyzing scat contents. Hair remains were identified to the most specific taxon possible with the assistance of a reference collection of hairs from mammals collected in the study area and an identification key (Moore et al. 1974). Bone fragments and teeth were also compared to a reference skeleton collection. The volumetric proportions of the contents were estimated visually and multiplied by the scat volumes to determine relative percentages of food items by volume. Additional procedures are presented in Zielinski (1981).

RESULTS

Plague Titers and Flea Occurrence

Four (M01,M07,F15,F21) of 13 martens captured were plague positive on 8 of 24 sampling occasions. Two of these individuals (F15,M01) were radio collared, and their ranges overlapped substantially (Fig. 1). The female, F21, was trapped once within the shared portion of home ranges of the previous two martens. Trapping data suggests that M07 occupied an area exclusive of the other three martens (Spencer 1981).

The antibody titer of three martens (M01,M07,F15) was tested a minimum of three times between August 1979 and May

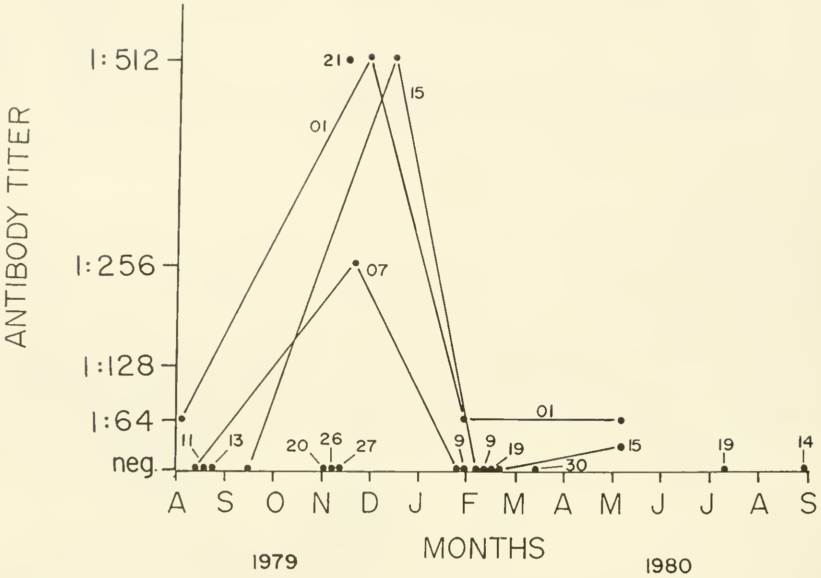

Fig. 2. Monthly distribution of marten plague titers from August 1979 to September 1980.

1980 (Fig. 2). Each expressed a titer peak of 1:256 to 1:512 in November or December. Although sampled only once, F21 expressed a titer of 1:512 during this time as well. Three other martens sampled during this same period, however, were negative.

Seventy fleas were collected from 13 martens (6F:7M) on 20 occasions (Table 1). Seven species in five genera were identified. Fleas were collected from all regions of the marten's body and during all seasons of the year. The flea, *Chaetopsylla floridensis*, is monoxenous to martens and was collected for the first time in California during the present study. All other fleas found occur more commonly on rodents. *Monopsyllus ciliatus*, a chipmunk flea, was the most common represented by 39 individuals. Flea species were easily distinguishable as warm or cold season parasites on martens. *Monopsyllus wagneri*, *Megarthoglossus* sp., and *Orchopeas nepos* were typical winter fleas collected between 5 November and 13 March. *Monopsyllus eumolpi*, *Monopsyllus ciliatus*, and *Oropsylla idahoensis* were collected only between 5 May and 5 September.

Food Habits

Thirty-six different food items were identified from 300 scats. Mammals composed 76.1% of the total annual diet, reaching a high of 87.9% during the winter. Rodents formed the largest portion of the mammal category, representing 62.1% of the annual diet and 64.2% during the summer. Because rodents are the primary hosts of plague-bearing fleas, the discussion of marten food habits will focus on these prey. A more complete description of marten food items at Sagehen is summarized by Zielinski et al. (1983).

Microtines (the montane vole, *Microtus montanus*, and the long-tailed vole, *M. longicaudus*) were the most common rodent prey, composing 23.7% of the annual diet (Table 2). Their use by martens was not confined to a particular season.

Most other mammalian prey were distinguished as either summer or winter food items. Chipmunks, golden-mantled ground squirrels (*Spermophilus lateralis*), California ground squirrels (*S. beecheyi*), and Belding ground squirrels (*S. beldingi*) were taken only during the snow-free period of the year. Chipmunks and golden-mantled ground squirrels were the most frequent prey, averaging 33.3% of the diet during this period. Conversely, the chickaree (*Tamiasciurus douglasii*), snowshoe hare (*Lepus americanus*), northern flying squirrel (*Glaucomys sabrinus*), and deer mouse (*Peromyscus maniculatus*) were primarily winter foods.

DISCUSSION

Titer Variance

Although most martens expressed a peak in antibody titer in late fall or early winter, antibodies were not detected in several individuals. Martens M20, M26, and M27 each had negative titers during November when martens M01, M07, F15, and F21 exhibited their highest titers. Several explanations for this result are possible. First, the three martens in which antibodies were undetected were all captured in the extreme northern boundary of the study area, at least 3 km from other marten captures. Plague may have either been distributed patchily within the study area and the martens in question lived within an uninfected area, or plague may have been moving through the region in a northerly direction and had not yet infected rodents in the area in which the martens foraged. Also, these three martens may have had recent exposure to plague and antibodies may have been too low to detect using the Nobuto strip technique. Finally, there may be a high degree of variation in the reaction of individual martens to plague exposure. Little is known of antibody response in martens, but responses have been shown to vary greatly from one individual to another in other predators and rodents (Barnes 1982).

Inferring Predator-Prey Interactions via Flea Fauna

Although the identification of marten fleas broadened the scant records of marten ectoparasite fauna (de Vos 1957, Eads et al. 1979), these data were also useful in deducing interactions between marten and their prey. Fleas are relatively host specific, parasitizing a subfamily, genus, or species of host (Pollitzer 1954:638). Because martens acquire fleas while consuming prey or searching burrows and nests, it is possible to infer the type of prey the martens hunt on the basis of their ectoparasite fauna. This information is useful in verifying food habits information obtained by scat analysis and in documenting exposure to rodents that are known plague reservoirs.

TABLE 1. Fleas recovered from martens at Sagehen Creek from July 1979 to September 1980.

Species	Date	M	F	Usual host(s)
Megarthroglossus sp.	24 Jan		1	Cricetine rodents (probably deer mouse)[b]
Monopsyllus wagneri	1 Feb		1	deer mouse[b]
M. ciliatus	5 May	1	2	chipmunks (except yellow pine)[b]
	4 June	3	8	
	24 June		1	
	29 Jul	2	3	
	4 Aug	3	6	
	17 Aug		2	
	18 Aug	1	1	
	20 Aug	2	2	
	5 Sep	1	1	
M. eumolpi	26 Jun	1		yellow-pine chipmunk[b]
	4 Aug	1		
	20 Aug	1		
Orchopeas nepos	5 Nov		1	chickaree[b]
	13 Mar		1	
Oropsylla idahoensis	4 June		1	golden-mantled ground squirrel[a]
	29 Jul	1		
Chaetopsylla floridensis	11 Nov	2	3	pine marten[b]
	29 Nov	2		
	16 Dec		1	
	24 Jan	2	4	
	2 Feb		1	
	11 Feb	3	2	
	13 Feb	1	1	
Totals		27	43	

[a] Barnes (1982)

[b] B. Nelson (pers. comm.)

Monopsyllus wagneri (deer mouse flea), *Megarthoglossus* sp. (mouse flea, most likely deer mouse nest flea) (Nelson, pers. comm.), and *Orchopeas nepos* (chickaree flea) were collected from martens during winter. The association of martens with these rodent hosts is also supported by their abundant remains found in scats of this period. Conversely, the fleas *Monopsyllus eumolpi*, *M. ciliatus*, and *Oropsylla idahoensis* were collected from martens during the snow-free period and are normally found on the yellow-pine chipmunk, other chipmunks, and the golden-mantled ground squirrel, respectively. Again there is a similarity between the flea's usual hosts and the marten's summer diet as determined by scat analysis.

Despite these associations, predicting marten food habits from flea species occurrence has several drawbacks. Species that are common prey may not be represented by their fleas. In this study, the fleas of snowshoe hares and voles were not found on martens. This is especially unusual for voles, considering their importance in the diet throughout most seasons. Eads et al. (1979) also found lagomorph fleas absent from martens in Colorado despite their abundance in a free-living state. In addition, the life cycle information necessary to determine the duration of flea persistence on a marten is lacking. Inferences about seasonal marten diets are inconclusive without this knowledge. Finally, the host specificity of many fleas is unknown. As the array of suitable hosts increases, the value of a flea in predicting specific prey eaten or hunted diminishes.

Inferring Plague Hosts via Flea Fauna and Plague Titers

Martens include many rodent species in their diet, but most evidence implicates ground-dwelling sciurids (chipmunks and ground squirrels) as the source of the marten's exposure to plague. Members of the genera *Eutamias* and *Spermophilus* are common hosts of plague-bearing fleas throughout the range of the disease in North America (Barnes 1982), and plague has been demonstrated in all species within these genera that occur at Sagehen Creek (Nelson 1980). Similarly, seasonal changes in seropositive badger (*Taxidae taxus*) titers were found to correlate with predation on the plague-susceptible Townsend ground squirrel (*Spermophilus townsendi*) in Idaho (Messick et al. 1983). Members of other genera upon which marten prey at Sagehen have been shown to be either somewhat refractory to the disease (i.e., *Tamiasciurus*, Nelson 1980, *Peromyscus* and *Microtus*, Bacon and Drake 1958, Hudson and Kartman 1967, Hubbert and Goldenberg

Table 2. Mammalian prey of the pine marten at Sagehen Creek 1979–1980, presented as total volume of 300 scats.

	1 Dec–1 Mar	2 Mar–25 Apr	26 Apr–1 July	2 July–1 Sept	2 Sept–30 Nov	Total
No. scats	91	61	76	25	47	300
No. items	138	96	125	59	84	502
Prey items						
Microtus spp.	37.4	5.2	33.2	4.5	18.3	23.5
Tamiasciurus douglasii	13.9	29.8	3.5	1.1	3.1	11.3
Spermophilus lateralis		1.8	13.9	25.2	10.9	8.3
Lepus americanus	18.8	10.0	0.7	1.9	0.9	7.7
Eutamias spp.	2.7		8.6	18.8	3.0	5.4
Glaucomys sabrinus	5.6	13.1			2.0	4.6
Peromyscus maniculatus	8.5	7.8	1.0		2.1	4.5
Scapanus latimanus		3.2	5.0	5.9	7.2	3.5
Thomomys monticola	2.3		2.1	7.2	0.2	2.0
Sorex spp.			4.0		3.2	1.5
Odocoileus hemionus		0.4	1.5		5.6	1.2
Spermophilus beldingi				4.7		1.0
Spermophilus beecheyi		0.5		0.9	3.0	0.2
Unidentified *Spermophilus*			3.5			1.0
Marmota flaviventris			0.2			0.1
Erethizon dorsatum		0.1				0.1

1970) or data on their susceptibility are lacking (i.e., *Glaucomys, Thomomys*) (Nelson 1980).

The time of the year that martens were seropositive also attests to their interactions with ground-dwelling sciurids. The highest titers occurred during November and December. Nevertheless, these peaks represent the decline phase of a higher response peak (probably greater than 1:1080) that would have been evident had these individuals been sampled in September or October (B. Nelson, pers. comm.). If marten antibody responses are similar to those in mongoose (*Herpestes auropunctatus*), these titer peaks typically should occur about one month after exposure (Meyer et al. 1965). Thus, if this assumption is correct, martens most likely contracted plague in August or September. This is in agreement with the annual escalation of plague activity during late summer in northern California (B. Nelson, pers. comm, Murray 1971) and occurs when martens are feeding primarily on chipmunks and ground squirrels. Because these rodents as a group are highly susceptible to plague, and because they compose a much greater component of the marten diet in northern California than elsewhere (Zielinski et al. 1983), pine martens may play a greater role in the ecology of plague in California than elsewhere.

Acknowledgments

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Literature Cited

Bacon, M., and C. H. Drake. 1958. Comparative susceptibility of various species of mice native of Washington to inoculation with virulent strains of *Pasteurella pestis*. J. Inf. Dis. 102:14-22.

Barnes, A. M. 1982. Surveillance and control of bubonic plague in the United States. Symp. Zool. Soc. London 50:237-270.

de Vos, A. 1957. Pregnancy and parasites of marten. J. Mammal. 38:412.

Eads, R. B., E. G. Campos, and A. M. Barnes. 1979. New records for several flea (Siphonaptera) species in the United States, with observations on species parasitizing carnivores in the Rocky Mountain region. Proc. Entomol. Soc. Washington 81:33-42.

Hubbert, W. T., and M. I. Goldenberg. 1970. Natural resistance of plague: genetic basis in the vole (*Microtus californicus*). Amer. J. Trop. Med. Hyg. 19:1015-1019.

Hudson, B. W., and L. Kartman. 1967. The use of the passive hemagglutination test in epidemiological investigations of sylvatic plague in the United States. Bull. Wildl. Dis. Assoc. 3:50-59.

Marchette, N. J., D. L. Lungren, D. S. Nicholes, J. B. Bushman, and D. Vest. 1962. Studies on infectious diseases in wild animals in Utah. II. Susceptibility of wild mammals to experimental plague. Zoonoses Res. 1:235-250.

Messick, J. P., G. W. Smith, and A. M. Barnes. 1983. Serological testing of badgers to monitor plague in southwestern Idaho. J. Wildl. Dis. 19:1-6.

Meyer, K. F., D. McNeill, and C. M. Wheeler. 1965. Results of a preliminary serological survey of small mammal populations for plague on the island of Hawaii. Bull. WHO 33:809-815.

Moore, T. D., L. E. Spence, and C. E. Dugnolle. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Dept. 177 pp.

Murray, K. F. 1964. The evolution of plague control in California. Proc. Second Vert. Pest Control Conf. Anaheim, California, pp. 143-149.

______. 1971. Epizootic plague in California, 1965-1968. Bureau of Vector Control, California Dept. of Public Health. 76 pp.

Nelson, B. C. 1980. Plague studies in California—the roles of various species of sylvatic rodents in plague ecology in California. Pages 89-96 *in* J. P. Clark, ed., Proc. 9th Vert. Pest Conf., Fresno, California, 4-6 March 1980.

Poland, J. D., and A. M. Barnes. 1979. Plague. Pages 515-559 *in* J. H. Steele, ed., CRC Handbook series on Zoonoses, section A: bacterial, rickettsial, and mycotic diseases. Vol. 1. CRC Press. Boca Raton, Florida.

Pollitzer, R. 1954. Plague. World Health Org. Monog. Series 22. 698 pp.

Rust, J. H., Jr., D. C. Cavanaugh, R. O'Shita, and J. D. Marshall, Jr. 1971. The role of domestic animals in the epidemiology of plague. I. Experimental infection in dogs and cats. J. Infect. Dis. 124:522-526.

Spencer, W. D. 1981. Pine marten habitat preferences at Sagehen Creek, California. Unpublished thesis. Univ. of California, Berkeley. 120 pp.

Wolff, K. L., and B. W. Hudson. 1974. Paper-strip blood sampling technique for the detection of antibody to the plague organism *Yersinia pestis*. Appl. Microbiol. 28:323-325.

Zielinski, W. J. 1981. Food habits, activity patterns and ectoparasites of the pine marten at Sagehen Creek, California. Unpublished thesis. Univ. of California, Berkeley. 121 pp.

Zielinski, W. J., W. D. Spencer, and R. H. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. J. Mammal. 64:387-396.

BODY FAT, BODY WATER, AND TOTAL CALORIC VALUE OF UINTA GROUND SQUIRRELS

James A. Gessaman[1]

Abstract.— The weight of body water and fat-free dry weight of Uinta ground squirrels (*Spermophilus armatus*) is given as a function of body weight. Body fat is presented as a function of body weight and body length. An equation for calculating the total caloric content of Uinta ground squirrels is given.

Fat index (weight of fat/fat-free dry weight) values of juveniles increased from 0.11 to 0.22 from 5 June to 28 July. In male yearlings and adults the fat index increased about 8 to 9 times in the latter half of June and early July.

Uinta ground squirrels (*Spermophilus armatus*) spend about 8.5 months of their annual cycle in hibernation. In northern Utah adult squirrels begin entering hibernation in July, and all squirrels have disappeared by early September (Knopf and Balph 1977). Fat is utilized as the primary source of energy during hibernation. This study measured the body fat of squirrels over several weeks prior to hibernation.

Methods

Thirty-eight male (ranging in body weight from 54.7 to 549.0 g) and 20 female (ranging from 57.4 to 554.0 g) Uinta ground squirrels were trapped along the Sinks Road in Franklin Basin, Cache County, Utah. They were transported to the laboratory and asphyxiated with carbon tetrachloride fumes, weighed, and stored in a freezer at –18 C. Weeks later, they were thawed, cut open, and desiccated to constant weight by freeze drying for 5 to 7 days. Each dried carcass was cut into smaller pieces, the fat content of each was extracted in a Soxhlet apparatus using petroleum ether (B.P. 60–80 C) as the solvent, and then each carcass was dried to constant weight in a hot-air oven at 80 C. The weight of body water was considered equal to the body weight at capture minus the vacuum-dried weight. The weight of body fat was equated with the vacuum-dried weight minus the dry weight of the fat-extracted carcass (i.e., the fat-free dry weight).

Body length and head width were measured, respectively, from the tip of the nose to the tip of the tail and at the widest point on the head, just posterior to the eyes.

A stepwise multiple regression analysis was used to derive equations relating each of the three parameters (body water, body fat, and fat-free dry weight) to body weight, body length, and head width.

Fat-extracted carcasses were ground in a Wiley mill and samples bombed in a Parr adiabatic bomb calorimeter.

Results and Discussion

The accuracy of predicting body water (B_{H_2O}) and fat-free dry weight (FFDW) from three variables (body weight, body length, and head width) was not significantly better than that from body weight alone:

(1) $B_{H_2O} = 37.48 + 0.5286\ BW \qquad r^2 = 0.933$

(2) $FFDW = 0.8149 + 0.2327\ BW \qquad r^2 = 0.958$

Where B_{H_2O}, FFDW and BW are in grams

The equation related body fat (BF) to both weight and body length (BL) and the highest r^2 value:

(3) $BF = 137.23 + 0.5342\ BW - 0.9488\ BL \qquad r^2 = 0.853$

Where BF is in grams and BL is in mm.

The coefficient of determination (r^2) between BF and body weight alone was 0.645.

The mean g-caloric value of the fat-free dry carcasses of 10 male and 9 female squirrels was 4601 kcal/g (SD = 573) and 4353 kcal/g (SD = 824), respectively. The total ca-

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TABLE 1. Mean fat index of Uinta ground squirrels captured in Cache County, Utah.

Date of capture	Mean fat index (Weight of fat/fat-free dry weight) ± SD of			
	Juveniles	Yearlings and adults		
		Males	Females	
			Not nursing	Nursing
5 June	0.11 ± .05 N = 9			
12 June	0.04 ± .00 N = 3	0.11 ± .03 N = 11	0.23 ± .00 N = 2	0.09 ± .06 N = 3
4 July	0.10 ± .03 N = 2	1.02 ± .04 N = 3	0.83 N = 1	
8 July	0.12 ± .09 N = 3	.88 ± .57 N = 5	0.76 ± .15 N = 2	
15 July	0.22 ± .12 N = 6			
28 July	0.22 ± .08 N = 7			

loric value (TCV in kcal) of a Uinta ground squirrel can be estimated from its body weight and body length from Eq. 4.

(4) $\mathrm{TCV} = 9.3\,\mathrm{BF} + \mathrm{FFDW} \times (4601 \text{ for males or } 4353 \text{ for females})$,
where BF and FFDW are computed from Eq. 3 and Eq. 2, respectively.

In the first half of June the fat index (weight of fat/fat-free dry weight) for yearling and adult squirrels and juveniles is not significantly different, but the rate of fat deposition within the next 30 days is about five times greater among yearlings and adults (Table 1), which normally begin to enter hibernation in early July.

Fat indices of males and females in my study were not significantly different, but the sample sizes are probably too small to uncover any real differences. In mid-June the fat index of lactating females ($\bar{x}$ = .092; SD = .064) was significantly lower (t = 3.83, dF = 2; p = 0.06) than that of nonlactating females ($\bar{x}$ = .233; SD = .002).

The body water index (weight of body water/weight of fat-free dry weight) for juveniles ($\bar{x}$ = 3.80; SD = 0.102) is significantly greater (t = 12.99; dF = 20; $p < .001$) than for yearlings and adults ($\bar{x}$ = 2.821; SD = 0.275) in the first half of June, and remains higher for the next month.

ACKNOWLEDGMENTS

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LITERATURE CITED

KNOPF, F. L., AND D. F. BALPH. 1977. Annual periodicity of Uinta ground squirrels. Southwest Naturalist 22:213–224.

FAT DEPTH AT THE XIPHOID PROCESS—A RAPID INDEX TO DEER CONDITION[1]

Dennis D. Austin[2]

ABSTRACT.— Measurement of the fat depth adjacent to the xiphoid process is described for mule deer. The index was determined sensitive to changes in physical condition of hunter-harvested mule deer.

Good physical condition of mule deer (*Odocoileus hemionus*) in fall is important to winter survival and optimal reproduction (Julander et al. 1961, Mautz 1978). Fat storage that reflects the annual nutritional cycle (Wallmo and Regelin 1981) peaks in fall (Anderson et al. 1972) and is a measure of summer habitat quality (Kistner et al. 1980). Although numerous carcass fat measurements have been reported (Anderson 1981), most require internal parts (not usually available from field-dressed deer at checking stations) and laboratory procedures and were designed for use with whole carcasses. At checking stations, where large samples can be collected, only eviscerated carcass weight and subcutaneous fat remain obtainable indexes. Although relatively few deer are needed for accurate mean eviscerated carcass weight (Anderson et al. 1972), weight appears a poor measure of condition because it is not correlated with other fat indexes used in assessments (Anderson et al. 1969).

Of various fat deposits, subcutaneous fat is deposited last and used first, and is only found on deer in good condition (Harris 1945). Thus, measurements of subcutaneous fat should be taken during the fall when physical condition is optimal (Mautz 1978, Wallmo and Regelin 1981). Measurement of back fat has been reported (Anderson et al. 1972), but requires skinning considerable portions of the rump. Experience in Utah has, understandably, shown most hunters unwilling to cooperate. Measurement of fat at the base of the sternum, which is often cut by hunters, is easy and presents no problem with hunter cooperation. This paper reports the use of this technique for hunter-harvested deer in late October.

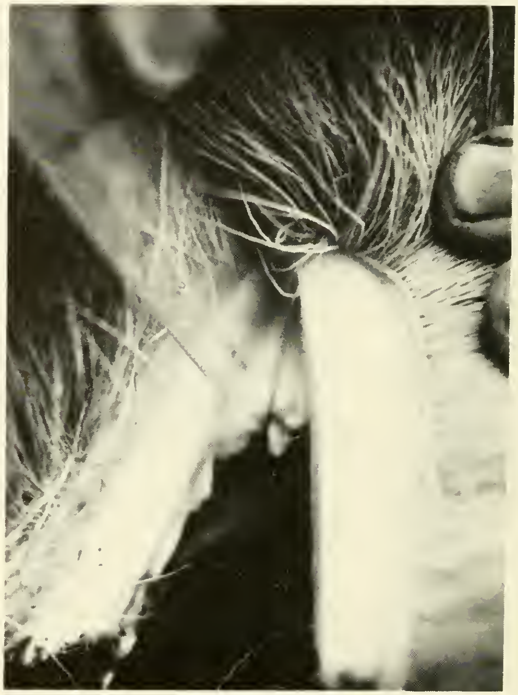

Fig. 1. Slit through the xiphoid process and connective tissues.

METHODOLOGY

Eviscerated carcasses are slit to the base of the sternum and through the xiphoid process (xiphisternum), the posterior segment of the sternum usually being less than 5 cm in length (Fig. 1). Fat depth, determined with a clear rule and read to the nearest millimeter, is measured adjacent and perpendicular to the xiphoid process between the skin and the next tissue layer. The mean depth observed along 2–3 cm of the slit fat strip immediately below the junction of the xiphoid process and

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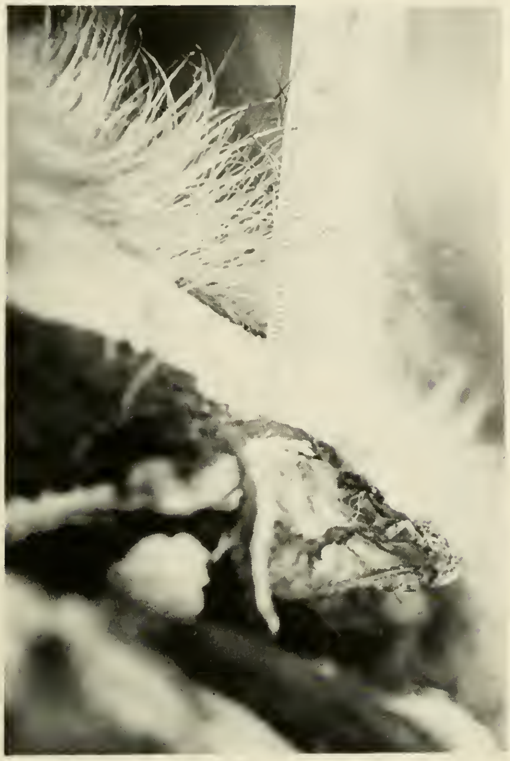

Fig. 2.—Measurement of fat depth adjacent to the xiphoid process.

the sternum is recorded (Fig. 2). Often a thin layer (<1.0 mm) of flesh is observed between the fat layer and the xiphoid process and marks the boundary for the measurement. On other deer the cartilage of the xiphoid process is the boundary. Occasionally deer in excellent condition have two or three layers of fat and flesh. Layering is uncommon, however, and only the outer layer of fat is measured. Usually, fewer than 30 seconds is required for individual measurements.

Carcasses previously cut through the xiphoid process are more difficult to measure because of bloody coloration, dirt, tissue separation, expansion and dehydration, and difficulty in determining the fat segment corresponding to the xiphoid process. Nevertheless, the measurement is essentially the same with a fresh cut made across the fat layer to aid accuracy. It should be noted that, because of these difficulties, many such deer cannot be measured accurately and are excluded from the sample.

MEASUREMENT PRECISION

Measurement variation of different investigators was determined using eight trained personnel at a checking station. Fat depths of 25 deer ranging in age from ½ to 4½ years were measured. The xiphoid process and fat layer were cut only once and each observer measured the cut strip with individual rules. To eliminate between-observer bias, hand signals rather than vocal communication were used to relay measurements to the person recording. Results showed high precision for mean fat depths ranging from 1 to 10 mm, with 23 of 25 deer having standard deviations of less than 1.0 mm (Table 1). The 2–3-cm long fat strip in most deer is quite uniform in thickness. Occasionally, however, this strip is wedge shaped and varies several millimeters, as with deer 19 (Table 1), where the strip varied 5–12 mm. In such cases the mean is more difficult to determine.

During 1981 and 1982 two checking stations were run simultaneously at nearby locations. Deer checked at the stations were harvested from the same areas and herd (Utah deer unit 13—Vernon), and no differences would be expected between samples. Fat depths were measured by 2–3 observers at each station on bucks whose ages were determined on-site to be yearling, 2½, or 3½+ years. Results showed no significant differences ($P<.05$) between sites within age classes (Table 2). Indeed, with good sample numbers in the yearling age class, differences in mean depths between sites were less than .4 and .1 mm for 1981 and 1982, respectively.

VARIABILITY IN DEPOSITION

Variability in fat deposition within age classes increased with animal age (Table 3). For yearling bucks a mean standard deviation of 2.5 mm was determined, increasing to 2.7 mm for deer 2½ years, and 3.1 mm for older deer. Even though mean fat depth exhibited considerable change between years, the variability of the index showed little fluctuation, particularly in the yearling age class. At 90 percent probability of detecting differences ($P<.05$) between yearling age groups differing in fat depth by 1 mm, a sample size of about 55 is needed, and by 2 mm about 15.

Table 1. Variability of fat depth measurements (mm) between eight observers.

Deer No.	Sex	Age (years)	Mean	Range	SD
1	M	1½	7.25	6–8	0.71
2	M	1½	4.75	4–5	0.46
3	F	1½	5.63	5–6	0.52
4	M	1½	5.88	5–7	0.64
5	F	3½	8.38	7–9	0.74
6	M	1½	6.88	6–8	0.64
7	M	1½	4.88	4–5	0.35
8	M	1½	1.13	1–2	0.35
9	M	1½	7.63	6–9	1.15
10	M	1½	4.38	4–5	0.52
11	M	1½	7.38	6–8	0.74
12	M	1½	7.00	6–8	0.76
13	M	1½	4.50	4–5	0.53
14	M	2½	9.63	9–10	0.52
15	M	1½	5.13	5–6	0.35
16	M	1½	9.00	8–10	0.76
17	M	1½	5.88	5–8	0.99
18	M	½	1.75	1–2	0.46
19	M	1½	8.63	6–11	1.60
20	M	2½	9.63	9–10	0.52
21	M	1½	2.13	2–3	0.35
22	M	1½	4.50	4–5	0.53
23	M	1½	1.00	1	0
24	M	1½	2.25	2–3	0.46
25	F	3½	3.25	2–4	0.89

Generally, significant differences ($P<.05$) in fat depth occurred between age classes (Table 3). In all comparisons, yearlings and older deer were different and, in four of five comparisons, yearlings were different from deer 2½ years of age. In only three of five comparisons were deer 2½ and 3½+ years different. It would be expected, with adequate sample sizes, that most, if not all, age classes would differ significantly.

Changes in fat deposition between years (Table 3) were found to be significant for yearlings ($P<.05$). Fall 1980 was an exceptional year for fall forage, especially berry production, and was reflected in increased fat deposition that was significantly ($P<.05$) greater than that in 1981, a poor forage year. Differences ($P<.05$) were also determined between deer units (Table 3). Deer unit 13, with limited high-quality summer range, produced yearling deer having considerably less subcutaneous fat than deer from unit 23B (Current Creek), where summer range is extensive.

Discussion and Application

The increased variability of fat deposition of buck deer older than yearlings and the difficulty in obtaining those samples suggests the technique be directed primarily to yearlings. A suggested rating scale for yearling bucks is 0–2 mm fat depth as poor physical condition, 2–4 mm as fair, 4–6 mm as good, 6–8 mm as very good, and 8+ mm as excellent. Measurements taken on does and fawns

Table 2. Variability of fat depth measurements (mm) on buck deer taken from two sites on Utah deer unit 13 (Vernon).[1]

	1981						1982					
	Site 1			Site 2			Site 1			Site 2		
Age	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
1½	100	3.6	2.3	51	4.0	2.9	51	4.9	2.0	36	5.0	2.6
2½	9	6.3	2.3	13	7.5	2.5	6	5.2	3.2	6	7.0	4.3
3½+	8	7.8	3.4	5	9.6	2.6	2	14.0	1.4	0	–	–

[1] No significant differences ($P<.05$) between sites within age classes were found.

TABLE 3. Fat depth (mm) of buck deer by age class.

	Utah deer unit 13 (Vernon)								
	1980			1981			1982		
Age	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
1½	41	5.3^{anx}[1]	2.6	151	3.7^{aox}	2.5	85	5.0^{anx}	2.2
2½	6	10.7^{bn}	2.5	22	7.0^{bnx}	2.4	12	6.1^{aox}	3.7
3½ +	10	14.3^{cnx}	3.6	13	8.5^{box}	3.1	2	14.0^{bnx}	1.4

	Utah deer unit 23B (Current Creek)								
	1980			1981			1982		
Age	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
1½	23	7.9^{any}	2.8	85	6.0^{aoy}	2.5	69	6.0^{aoy}	2.7
2½		no data		5	9.4^{bny}	2.1	6	8.0^{bnx}	2.8
3½ +	5	15.6^{bnx}	5.4	11	14.0^{bny}	4.6	4	14.0^{cnx}	6.3

[1] Differences ($P<.05$) between age classes within years and units are denoted by letters a,b,c; differences between years within age classes and units are indicated by letters n,o; and differences between units within years and age classes are indicated by letters x,y.

would also be expected to yield good results where samples are adequate. Moreover, sample sizes for does and fawns may be smaller than those needed for bucks because of the nonsynchronous rutting behavior that increases fat depth variability of bucks (Kistner et al. 1980).

Use of this index could detect annual changes in late summer-fall forage conditions as they affect the deer population's physical condition. Differences between units could serve as a comparison for adequacy of summer ranges. Fluctuations in the deer population and corresponding changes in fat deposition could be correlated with the forage resource, thereby providing a measure of balance between population size and forage resources. Data could also be used to adjust harvest and to avoid possible excessive winter losses during years when physical condition in fall is determined to be poor and population is high.

LITERATURE CITED

ANDERSON, A. E. 1981. Morphological and physiological characteristics. Chap. 2, pages 27–97 *in* Mule and Black-tailed deer of North America. Wildlife Management Institute Book, Univ. of Nebraska Press, Lincoln. 605 pp.

ANDERSON, A. E., D. E. MEDIN, AND D. C. BOWDEN. 1972. Indices of carcass fat in a Colorado mule deer population. J. Range Manage. 36:579–594.

ANDERSON, A. E., D. E. MEDIN, AND D. P. OCHS. 1969. Relationships of carcass fat indices in 18 wintering mule deer. Proc. West. Assoc. State Game and Fish Comm. 49:329–340.

HARRIS, D. 1945. Symptoms of malnutrition in deer. J. Wildl. Manage. 9:319–322.

JULANDER, O., W. L. ROBINETTE, AND D. A. JONES. 1961. Relation of summer range condition to mule deer herd productivity. J. Wildl. Manage. 25:55–60.

KISTNER, T. P., C. E. TRAINER, AND N. A. HARTMANN. 1980. A field technique for evaluating physical condition of deer. Wildl. Soc. Bull. 8:11–17.

MAUTZ, W. W. 1978. Sledding on a bushy hillside: the fat cycle in deer. Wildl. Soc. Bull. 6:88–90.

WALLMO, O. C., AND W. L. REGELIN. 1981. Rocky Mountain and Intermountain habitats: food habits and nutrition. Chap. 10, Part 1, pages 387–398 *in* Mule and Black-tailed Deer of North America. Wildlife Management Institute Book, Univ. of Nebraska Press, Lincoln. 605 pp.

SHRUB RESEARCH CONSORTIUM FORMED

Arthur R. Tiedemann[1]

The Forest Service's Intermountain Forest and Range Experiment Station, the Utah Division of Wildlife Resources, Brigham Young University, and Utah State University announce the formation of a Shrub Research Consortium. Formed to promote, support, and coordinate programs of research and associated graduate education, the consortium will be located at the Shrub Sciences Laboratory, 735 North 500 East, Provo, Utah 84601. Activities will relate to (1) improvement and development of shrub plant materials; (2) methods of seeding, planting, culturing, and managing shrubs in natural settings; and (3) assisting where feasible with publishing and disseminating research results.

Specific goals of the consortium are:

1. Develop a program consisting of statements of research needs and priorities and current studies aimed at meeting those needs. The consortium may determine and set objectives, priorities, and guidelines for studies, based on interpretation of need, available funds, capabilities of institutions and personnel, and other work under way within or outside the consortium. Principal areas of shrub research will include, but will not be limited to: ecology, genetics, pathology, entomology, soils, hydrology, wildlife habitat, and livestock grazing.

2. Encourage proposals to conduct research from both member and nonmember institutions desiring to participate and capable of contributing appropriately to solving problems selected for study.

3. Arrange for printing and distributing publications and reports.

4. Sponsor seminars, conferences, symposia, and other meetings to coordinate research on wildland shrubs and to disseminate research results.

Applications for membership from organizations involved in wildland shrub research are encouraged.

For further information, contact the author.

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[1] Shrub Sciences Laboratory, Intermountain Forest and Range Experiment Station, 735 North 500 East, Provo, Utah 84601.

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UTAH FLORA: CHENOPODIACEAE

Stanley L. Welsh[1]

Abstract.— The Chenopodiaceae for Utah are revised. Descriptions of the family and of its genera and species are included. Keys to the genera, species, and infraspecific taxa are provided, along with pertinent discussion. Treated are 18 genera, 56 species, and 13 infraspecific taxa. Newly described taxa are *Atriplex canescens* (Pursh) Nutt. var. *gigantea* Welsh & Stutz, *Ceratoides lanata* (Pursh) J. T. Howell var. *ruinina* Welsh, and *Chenopodium capitatum* (L.) Asch. var. *parvicapitatum* Welsh. New nomenclatural combinations are: *Atriplex canescens* (Pursh) Nutt. var. *occidentalis* (Torr. & Frem.) Welsh & Stutz; *Atriplex gardneri* (Moq.) D. Dietr. — var. *bonnevillensis* (C. A. Hanson) Welsh, var. *cuneata* (A. Nels.) Welsh, var. *falcata* (Jones) Welsh, and var. *welshii* (C. A. Hanson) Welsh; *Atriplex patula* L. var. *triangularis* (Willd.) Thorne & Welsh; *Atriplex saccaria* Wats. var. *caput-medusae* (Eastw.) Welsh; *Zuckia brandegei* (Gray) Welsh & Stutz, and *Zuckia brandegei* var. *arizonica* (Standl.) Welsh.

Members of the Chenopodiaceae have long been regarded as taxonomically troublesome. Reasons for the difficulties involve reduction and simplification of floral parts leading to use of features of fruit, bracts, vegetative characters, and, more recently, phytochemistry as diagnostic tools. Problems are compounded due to introduction of many of the species from the Old World. Both taxonomic and nomenclatural difficulties occur within the taxa in the Old World, the plants having proved to be only somewhat less perplexing to Eurasian taxonomists than to American ones. Once introduced into the New World, the problems of adequate taxonomy and nomenclature are made more difficult because of lack of adequate specimens for comparison. Often literature is not available to make valid judgements, or is difficult to use because of language barriers. Only portions of the total variability of Old World taxa are introduced, and our view of morphological limits of the taxa differs from that held by taxonomists working with them in their home environments. Some indigenous taxa are made problematical by having Old World counterparts, from which they are segregated by diagnostic features that might be neglegible. Nomenclatural decisions are based on determinations made initially in Europe, some more than a century ago. Compilation and correlation of all data available often does not lead to clarification of taxonomic limits. Additionally, hybridization is known to occur in many indigenous taxa (e.g., the *gardneri* complex of *Atriplex*).

Plants of the Chenopodiaceae are of vast ecological importance due to their ablity to occupy saline or alkaline substrates. Lands with such substrates are abundant in Utah. The saline substrates of valley bottoms, bajadas, alluvial fans, and of many geological strata are sources of plants that are important for use by grazing and browsing animals, especially in autumn, winter, and early spring. Chenopods are often principal components, and many of them are utilized by sheep, cattle, horses, other domestic livestock, and wildlife. Perennial species of *Atriplex*, usually referred to as saltbush, are especially important browse plants on wildland ranges in Utah. The lambsquarter or pigweed, *Chenopodium album*, is a serious weed of gardens but is not confined to them. Russian thistle and halogeton are weedy species that occupy disturbed sites similar to those supporting the cheatgrass, *Bromus tectorum* L. Both are used for food, supplementally, on winter grazing areas by sheep and by cattle. However, halogeton contains high concentrations of oxalates, which, when eaten in quantity, result in calcium shock and subsequent death. Serious losses of sheep have occurred since introduction of this attractive annual in the 1930s in Nevada. Greasewood is also a potential oxalate poisoner, but is eaten, especially by cattle, in some years without apparent harm. Annual species of *Chenopodium* and *Atriplex* can become poisonous through accumulation of nitrates in heavily fertilized cultivated lands.

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In Utah the family consists of 18 genera (6 entirely introduced, and 3 with both New and Old World representatives), 56 species, and 13 varieties. Eighteen (or 26 percent) of the taxa (all of them species) are introduced. This is a high proportion of introductions, much higher than for most families of comparable or larger size. Because of the abundance of saline habitats in Utah, many more introductions from elsewhere in the world should be expected.

Many of the species change colors in autumn, taking on themselves hues of red, red-orange, or purple, resulting in a subtle display of great beauty. The drab appearance of the growing season gives way to a pleasing glow, especially when viewed in early morning or evening light.

CHENOPODIACEAE

Goosefoot Family

Herbs, subshrubs, or shrubs, often succulent or scurfy; leaves simple, alternate or opposite, estipulate; flowers inconspicuous, monoecious, dioecious, polygamous, or perfect; calyx persistent, 1- to 5-lobed, enclosing the fruit, or lacking in some pistillate flowers; corolla none; stamens opposite the calyx lobes and as many or fewer; pistil with 1–3 stigmas, 1-loculed and 1-ovuled; fruit a utricle.

1. Leaves scalelike; stems fleshy; plants of saline pans and other salty sites 2
— Leaves well developed, not scalelike; stems not fleshy; plants of various habitats 3

2(1). Leaves alternate; plants woody at the base, mainly 3–8 dm tall .... *Allenrolfea*
— Leaves opposite; plants herbaceous, mainly 0.5–3 dm tall .... *Salicornia*

3(1). Leaves opposite, united at the base; sepals strongly imbricate, scarcely united, chartaceous; plants rare in western Utah .... *Nitrophila*
— Leaves alternate or rarely some opposite; sepals slightly if at all imbricate, herbaceous 4

4(2). Leaves or bracts of inflorescence tipped with a spine or a spinelike bristle 5
— Leaves and floral bracts not bristle or spine tipped 6

5(4). Leaves linear to subulate; bracts of inflorescence ovate-lanceolate, spine tipped; fruiting sepals winged on the back; flowers not embedded in hair .... *Salsola*
— Leaves sausagelike, abruptly spine tipped; bracts of inflorescence not different from the leaves; sepals ending in wings; flowers embedded in hair .... *Halogeton*

6(4). Leaves sub- or semicylindric to linear, usually fleshy 7
— Leaves with flattened blades, not especially fleshy 9

7(6). Shrubs, armed with thorny branchlets; staminate flowers in spikes, the pistillate flowers solitary and axillary .... *Sarcobatus*

— Shrubs or herbs, not armed; flowers perfect or both perfect and pistillate 8

8(7). Herbage villous-tomentose; plants low subshrubs .... *Kochia*

— Herbage glabrous and glaucous, or puberulent; plants annual or perennial, or if subshrubs then tall .... *Suaeda*

9(6). Plants densely white-hairy with at least some dendritic hairs, these becoming golden brown in age; shrubs of broad distribution .... *Ceratoides*

— Plants variously hairy or glabrous, but not as above; shrubs or herbs of various distribution 10

10(9). Flowers imperfect, the pistillate enclosed in 2 accrescent or connate bracts 11

— Flowers perfect or some also pistillate, all with sepals and not enclosed by paired bracts 14

11(10). Stigmas 4 or 5; plants green, cultivated potherbs .... *Spinacia*

— Stigmas 2; plants green, grayish, or yellow-green, not or seldom cultivated 12

12(11). Bracts dorsally compressed, variously tuberculate, smooth, or winged; pubescence of inflated hairs or none; plants shrubs or perennial or annual herbs; axillary rounded buds lacking .... *Atriplex*

— Bracts laterally compressed or 6- to 8-ribbed, lacking appendages; pubescence of simple or branched hairs; plants shrubby; axillary rounded buds present 13

13(12). Shrubs with divaricate often thorny branches; bracts with margins thickened, spongy within; pubescence of branched hairs .... *Grayia*

— Shrubs with erect nonthorny branches; bracts with margins not spongy thickened, either obcompressed or dorsiventrally compressed and 6-ribbed; pubescence of scurfy or moniliform hairs .... *Zuckia*

14(10). Plants more or less tomentulous; calyx transversely winged in fruit .... *Cycloloma*

— Plants glabrous, scurfy, pilose, or otherwise pubescent, but not or seldom as above; calyx not transversely winged in fruit, except in *Kochia* (q.v.), and then not tomentulous 15

15(14). Perianth developing conspicuous horizontal, scarious wings or armed with curved or uncinate spines 16

— Perianth lobes rounded or keeled on the back, lacking wings or spines 17

16(15). Perianth developing conspicuous, horizontal, scarious wings .... *Kochia*

— Perianth with lobes each armed with a curved or uncinate spine .... *Bassia*

17(15). Calyx becoming woody in age; ovary partly inferior; plants cultivated, rarely escaping .... *Beta*

— Calyx not woody; ovary superior; plants not or seldom cultivated 18

18(17). Calyx lobes 5, largely concealing to exposing the fruit; stamens usually 5; herbage glabrous or scurfy .... *Chenopodium*

— Calyx lobes 1–3, the fruit largely exposed; stamens 1–3; plants not scurfy 19

19(18). Leaves hastately lobed or if entire 4–12 mm long, the blades mainly 2–8 mm broad or more; calyx l-lobed; stamens 1; plants widespread, of many habitats .... *Monolepis*

— Leaves linear, 0.8–6 cm long, entire, 1–2 mm wide; calyx 1- to 3-lobed; stamens 1–3; plants of sandy, low-elevation sites .... *Corispermum*

ALLENROLFEA Kuntze

Succulent, glabrous subshrubs or shrubs; branches alternate, jointed; leaves reduced to fleshy scales, alternate; flowers perfect, sessile, borne spirally in 3s or 5s in axils of peltate bracts, arranged in cylindrical erect spikes; sepals reduced, 4- to 5-lobed; stamens 1 or 2, exserted; stigmas 2 or 3; utricle ovoid, flattened, the pericarp free, membranous.

Allenrolfea occidentalis **(Wats.) Kuntze** Iodine Bush. [*Halostachys occidentalis* Wats., type from Raft River Valley]. Plants mainly 3–8(12) dm tall, woody at least below, glabrous and more or less glaucous; stems constricted at the nodes, fleshy; leaves very short, obtusely triangular; spikes 6–30 mm long; calyx enclosing the fruit; seeds brown. Saline and alkaline pans, springs, and seeps, and in other saline sites, often with saltgrass, samphire, seepweed, and other halophytes, at 1380 to 1620 m in Beaver, Box Elder, Emery, Grand, Iron, Juab, Millard, Salt Lake, Tooele, Utah, and Wayne counties; Oregon and Idaho, south to California, Arizona, Texas, and Mexico; 25 (iv). The plants accommodate high soil salinity by including salt within the protoplast, giving the plant a salty flavor. Because of its salty flavor the plants are often referred to as "pickleweed."

ATRIPLEX L.

Monoecious or dioecious herbs or shrubs, often with scurfy (mealy) collapsed hairs; leaves alternate or opposite; flowers small, inconspicuous, borne in axillary clusters, glomerules, or in spicate panicles; staminate flowers with 3- to 5-parted calyx, bractless, with 3–5 stamens; pistillate flowers without a perianth and the pistil naked or rarely with a perianth, commonly enclosed within a pair of foliaceous bracts, enlarged in fruit, variously thickened and appendaged; styles 2; utricle with the pericarp free; seeds flattened, mainly erect. The genus is complex both taxonomically and nomenclaturally. It consists of native and introduced herbs and shrubs. Indigenous shrubby species form hybrids with all or most of their constituent taxa, wherever they come in contact. The resulting plasticity allows these remarkable plants to occupy numerous habitats, but poses problems that preclude a "neat" taxonomic treatment. The following keys are tentative at best.

HANSON, C. A. 1962. Perennial *Atriplex* of Utah and the northern deserts. Unpublished thesis. Brigham Young Univ. 133 pp.

THORNE, K. H. 1977. A revision of the herbaceous members of the genus *Atriplex* (Chenopodiaceae) for the state of Utah. Unpublished thesis. Brigham Young Univ. 78 pp.

1. Plants herbaceous annuals .... Key I.
— Plants woody, at least below, perennial .... Key II.

KEY I.

Plants herbaceous annuals.

1. Seeds of 2 types, black and brown; plants mainly introduced 2
— Seeds all alike, either black or brown; plants indigenous 5
2(1). Fruiting bracts orbicular or nearly so, the dorsal surfaces smooth, entire 3
— Fruiting bracts triangular to ovate or rhombic, the dorsal surfaces usually tubercled, denticulate to entire 4
3(2). Black seeds horizontal, enclosed in a membranous calyx; brown seeds vertical between very large bracts .... *A. hortensis*
— Black seeds vertical between small bracts; brown seeds vertical between large bracts .... *A. heterosperma*
4(2). Lowermost leaves ovate, dentate, sessile or short-petiolate .... *A. rosea*
— Lowermost leaves lanceolate, rhombic, triangular, or hastate, dentate or entire, petiolate .... *A. patula*

5(1). Plants dioecious, widely distributed in eastern Utah, rarely elsewhere .... *A. powellii*

— Plants monoecious, of various distribution 6

6(5). Fruiting bracts orbicular or nearly so, the margins denticulate to lacerate; plants of Washington County .... *A. elegans*

— Fruiting bracts various in outline, but, if orbicular, the margins entire and seldom if ever in Washington County 7

7(6). Lower leaves linear to lanceolate, sessile, not over 2.5 cm long .... *A. wolfii*

— Lower leaves rhombic, deltoid, or cordate, usually at least some petiolate 8

8(7). Fruiting bracts all stipitate, or some of them sessile to subsessile, when stipitate usually prominently tubercled; plants forming low, rounded clumps on saline substrates in eastern Utah .... *A. saccaria*

— Fruiting bracts all sessile or subsessile, variously tubercled or, if stipitate, as in *A. graciliflora*, the surfaces smooth; plants slender or clump forming, variously distributed 9

9(8). Fruiting bracts truncate and with 3 minute teeth apically; upper leaves sessile . ... *A. truncata*

— Fruiting bracts not truncate apically; upper leaves petiolate or subsessile 10

10(9). Fruiting bracts with margins dentate, foliaceous well below the apex, the surfaces sometimes with appendages .... *A. argentea*

— Fruiting bracts samaralike, orbicular, with a winged entire margin surrounding the seed; surfaces smooth .... *A. graciliflora*

KEY II.

Plants woody, at least below, perennial.

1. Leaves dentate (at least some); plants of Washington County 2

— Leaves entire; plants of various distribution 3

2(1). Plants monoecious; leaves green, ovate, irregularly and shortly dentate; weedy species near St. George .... *A. semibaccata*

— Plants dioecious; leaves silvery white, orbicular, definitely and coarsely toothed; indigenous .... *A. hymenelytra*

3(1). Leaf blades subhastate; shrubs to 30 dm tall; plants of Washington County 4

— Leaf blades attenuate to rounded basally; shrubs mainly less than 2 m tall; plants of various distribution 5

4(3). Branchlets terete .... *A. lentiformis*

— Branchlets angled .... *A. torreyi*

5(3). Bracts with 4 lateral wings or 4 rows of teeth; plants unarmed 6

— Bracts without lateral wings, merely tuberculate or smooth dorsally; plants sometimes thorny 8

6(5). Leaves more than 8 mm wide; bract tip with or without lateral teeth; canyons of the Colorado .... *A. garrettii*

— Leaves less than 8 mm wide; bract tip without lateral teeth; distribution various 7

7(6). Bracts more than 9 mm wide, with tips not exceeding the wings; staminate flowers yellow; shrubs to 2 m tall, widely distributed .... *A. canescens*

— Bracts less than 9 mm wide, with tips exceeding the wings; staminate flowers mostly brown; plants mainly 5–10 dm tall, of playas in western Utah .... *A. gardneri*

8(5). Plants with thorny branches; bracts foliose, united only basally, the surfaces smooth; staminate flowers yellow; widely distributed .... *A. confertifolia*

— Plants lacking thorny branches; bracts not foliose, at least one-third united and the surfaces with appendages; staminate flowers yellow or brown 9

9(8). Leaves 2–4 mm wide; bracts with appendages on lower one-third; staminate flowers in spikes; plants prostrate .... *A. corrugata*

— Leaves often more than 4 mm wide; bracts with appendages various; staminate flowers mainly in panicles; plants not or seldom prostrate 10

10(9). Leaves oblong-ovate to orbicular, more than 10 mm wide, the lowermost alternate; staminate glomerules very numerous; plants of San Juan County .... *A. obovata*

— Leaves linear to oblong, mainly less than 10 mm wide, or, if wider, the lowermost opposite; staminate glomerules merely numerous; plants of Great Basin and northern Colorado River drainage, less commonly in San Juan County .... *A. gardneri*

Atriplex argentea **Nutt.** Silver Orach. [*A. rydbergii* Standley, type from south of Moab]. Plants annual, monoecious; stems simple or freely branched; leaves petiolate or the upper ones subsessile, the blades 0.5–6 cm long, 0.4–5 cm wide, lance-ovate, lanceolate, deltoid, or cordate, runcinate to subhastate basally, obtuse to acute apically, entire or essentially so, scurfy (glabrous); staminate flowers with 5-parted calyx; fruiting bracts sessile, or subsessile, 4–5 mm long, 4–10 mm wide, the margin foliaceous below the apex, dentate to laciniate, the face smooth, tubercled, or crested; seeds ca 2 mm wide, brown. 2n = 18. Mat-atriplex, shadscale, and greasewood communities at 1125 to 1770 m in Duchesne, Emery, Kane, Rich, San Juan, Salt Lake (?), Sevier, Summit, and Uintah counties; widespread in western U.S. and Mexico; 20 (0).

Atriplex canescens **(Pursh) Nutt.** Fourwing Saltbush. [*Calligonum canescens* Pursh]. Dioecious or rarely monoecious shrubs, mainly 8–20 dm tall, not especially armed; leaves persistent, alternate, sessile or nearly so, 10–40 mm long, 2–8 mm wide, linear to oblanceolate, oblong, or obovate, entire, retuse to obtuse apically; staminate flowers yellow (rarely brown), in clusters 2–3 mm wide, in panicles; pistillate flowers borne in panicles 5–40 cm long; fruiting bracts 9–25 mm long and as wide, on pedicels 1–8 mm long, with 4 prominent wings extending the bract length, united throughout; surface of wings and body smooth or reticulate; wings dentate to entire; apex toothed; seeds 1.5–2.5 mm wide; 2n = 18, 36, or higher. Sandy, commonly non saline, sites in Joshua tree, blackbrush, greasewood, salt desert shrub, sagebrush, mountain brush, and pinyon-juniper communities at 670 to 2380 m, known in all Utah counties except Cache, Morgan, Rich, Wasatch, and Weber; Washington to Alberta and South Dakota, south to Mexico and Texas; 199 (xxiv). This species forms hybrids with *A. confertifolia* and *A. gardneri* varieties (see var. *bonnevillensis*). Materials from the type locality of the species in South Dakota is a low subherbaceous plant that differs from our shrubby tall material. In a strict sense the common phase of our plants seems best regarded at varietal status as ***A. canescens*** **var. *occidentalis*** **(Torr. & Frem.) Welsh & Stutz** comb. nov. [based on: *Pterchiton occidentale* Torr. & Frem in Frem. Rep. Rocky Mts. 318. 1846, type from the Great Salt Lake, and the autonym var. *occidentalis* established by *Obione occidentalis* var. *angustifolia* Torr. in Emory Bot. Mex. Bound. 2 (1):189. 1859]. A second more or less distinctive phase occurs within the distribution of var. *occidentalis*, but is restricted ecologically and differs morphologically from that variety. These dune plants were noted by Hanson (1962) as having bracts to 25 mm wide and elongated internodes. To these features can be added the presence of adventitious roots at buried internodes and a diploid chromosome number of 2n = 18. They are here designated as **var. *gigantea* Welsh & Stutz var. nov.** Ab *Atriplex canescens* var. *occidentalis* in bracteis majoribus internodiis longioribus radicibus adventitiis et chromosomatibus 2n = 18 differt. Type: USA Utah. Juab County; Lynndyl sand dunes, T35S, R4W, 8 Sept. 1965, S. L. Welsh & G. Moore 5126 (Holotype BRY; two isotypes distributed previously as *A. canescens*). Plants of var. *gigantea* grow in interdune valleys, where they are encroached upon by the following dune. They survive being buried as the dune advances by producing adventitious roots along the stem and by continued growth above the encroaching sand. The species is an important browse plant for both wildlife and domestic livestock. It is used in reclamation projects and might be found established at sites beyond its usual range and habitat latitude.

***Atriplex confertifolia* (Torr. & Frem.) Wats.** Shadscale [*Obione confertifolia* Torr. & Frem. in Frem., type from Weber County; *A. collina* Woot. & Standl.]. Dioecious spinescent shrubs, 3–8 dm tall; leaves persistent, alternate, with petioles 1–4 mm long; blades 9–25 mm long, 4–20 mm wide, orbicular to ovate, elliptic, or oval, entire, obtuse apically; staminate flowers yellow, in clusters 2–4 mm wide or in spikes to 1 cm long; inflorescence paniculate, 3–15 cm long; fruiting bracts sessile or subsessile, suborbicular to rhombic or elliptic, 4–12 mm long and wide, the surface smooth, lacking appendages; terminal teeth distinct, foliaceous, shorter than the bracts, entire or toothed below, spreading at maturity; seeds 1.5–2 mm broad. 2n = 18, 36, or higher. Gravelly to fine-textured soils in greasewood, mat-atriplex, other salt desert shrub, sagebrush, and pinyon-juniper communities at 850 to 2140 m, known in all Utah counties except Morgan, Rich, and Summit; Oregon east to North Dakota, south to California, Arizona, New Mexico, and Texas; 144 (xii). Shadscale forms hybrids with *A. canescens*, *A. garrettii*, *A. corrugata*, and *A. gardneri* varieties. This is a valuable browse plant for wildlife and livestock, especially sheep.

***Atriplex corrugata* Wats.** Mat-saltbush; Mat-atriplex. Dioecious, low, spreading shrubs, mainly 3–15 cm tall and 3–15 dm broad; leaves persistent, sessile, opposite below, alternate above, 3–18 mm long, 1–6 mm wide, linear to linear-oblanceolate, or oblong, entire, obtuse apically; staminate flowers yellow to brownish, in clusters 3–6 mm wide, borne in spikes 1–8 cm long; pistillate flowers in leafy bracteate spikes 5–15 cm long; fruiting bracts sessile or subsessile, 3–5 mm long, 4–6 mm wide, densely tuberculate (or smooth), entire or undulate, rounded to acute apically; seeds ca 1.5 mm wide. 2n = 36. Saline, usually fine-textured substrates derived from Mancos Shale, Tropic Shale, Morrison, Duchesne River, and other similar formations in mat-atriplex and Castle Valley saltbush communities at 1220 to 2150 m in Carbon, Emery, Garfield, Grand, Kane, San Juan (?), and Uintah counties; New Mexico and Colorado; 105 (viii). Mat-saltbush is known to form intermediates with both *A. confertifolia* and *A. gardneri* var. *cuneata*. This saltbush is a valuable browse plant on the sparsely vegetated clays and silts of eastern Utah, where it is often the only woody vegetation present.

***Atriplex elegans* (Moq.) D. Dietr.** Wheelscale Orach. [*Obione elegans* Moq.]. Annual herbs, the stems erect to ascending or prostrate-decumbent, mainly 1–6 dm tall, scurfy to glabrate; leaves mostly alternate, subsessile or shortly petiolate, 5–30 mm long, 2–8 mm wide, elliptic to spatulate, oblanceolate, oblong, or obovate, the base cuneate, entire to denticulate, densely scurfy; flowers monoecious, in axillary clusters; staminate flowers with a 3–5 parted perianth; fruiting bracts shortly stalked, compressed, united except at the thin margin, orbicular, 2–4 mm wide, the margins dentate, the terminal teeth often promiment, the faces smooth; seeds 1–4 mm wide, brown. Disturbed sites at ca 885 m in Washington County; California, Nevada, Arizona, New Mexico, Texas, and Mexico; 3 (0).

***Atriplex gardneri* (Moq.) D. Dietr.** Gardner Saltbush. [*Obione gardneri* Moq.; *A. nuttallii* Wats.]. Dioecious or monoecious shrubs or subshrubs, 1–10 dm tall, unarmed; leaves more or less persistent, alternate or opposite to subopposite, sessile to petiolate, linear to oblanceolate, obovate, spatulate, or orbicular, 5–55 mm long, 2–25 mm wide, entire (rarely dentate), retuse to obtuse or rounded apically; staminate flowers in spikes or panicles, 2–30 cm long, yellow or brown, in clusters 2–4 mm wide; pistillate flowers in spikes or panicles to 30 cm long; fruiting bracts 3–9 mm long, 2–9 mm wide, bearing tubercles or wings or the tubercles alligned in 4 rows or rarely smooth, the apex toothed and usually with 2 or more lateral teeth; seeds 1.5–2.5 mm wide, tan or brown. This is a widely distributed complex of intergrading genotypes of great plasticity. Plants of this complex occur commonly in saline fine-textured substrates in much of the western Great Plains and in the intermountain region. Diploids, triploids, tetraploids, and hexaploids (and higher polyploids, all multiples of the base number 9) are known within the complex, and hybrids are known between the constituents and the other woody species they contact, i.e., *A. canescens*, *A. confertifolia*, and *A. corrugata*. The treatment essentially follows the alignment of taxa suggested by Hanson (1962), with the exception that they are reduced to varietal status and var. *bonnevillensis* is placed within the *gardneri* phase and not with *A. canescens*. The use of the epithet *nuttallii* for this complex was reviewed by Hanson (1962), and, other problems aside, the name *A. gardneri* clearly has priority over *A. nuttallii* and must be used according to stipulations of the International Code. Within Utah there are six morphologically intergrading entities that seem worthy of taxonomic recognition.

1. Fruiting bracts with 4 lateral wings or rows of tubercles; plants of valley bottoms and playas in Juab and Millard counties .... *A. gardneri* var. *bonnevillensis*

— Fruiting bracts lacking lateral wings, the tubercles, when present, often more or less aligned; plants of various distribution 2

2(1). Lower leaves opposite or subopposite; plants prostrate to ascending, in eastern Utah 3

— Lower leaves alternate; plants ascending to erect, of various distribution 4

3(2). Leaves mainly 10–25 mm wide, grayish green; bracts 5–9 mm wide, heavily tuberculate; plants of the Uinta and Navajo basins .... *A. gardneri* var. *cuneata*

— Leaves mainly 4–12 mm wide, green; bracts 2–5 mm wide, not tuberculate or the tubercles very short; plants of Daggett County .... *A. gardneri* var. gardneri

4(2). Staminate flowers mostly brown; fruiting bracts with apical teeth half united, lacking lateral teeth; plants of Great Basin and Rich County .... *A. gardneri* var. *falcata*

— Staminate flowers mostly yellow; fruiting bracts with apical teeth free, subtended by lateral teeth; plants of various distribution 5

5(4). Leaves mainly 5–15 times longer than wide; fruiting inflorescences spicate; plants of Grand County .... *A. gardneri* var. *welshii*

— Leaves mainly less than 5 times longer than wide; fruiting inflorescences paniculate; plants of broad distribution .... *A. gardneri* var. *tridentata*

Var. ***bonnevillensis*** **(C. A. Hanson) Welsh** comb. nov. Bonneville Saltbush. [based on: *Atriplex bonnevillensis* C. A. Hanson Studies Systematic Botany 1:2. 1962]. Greasewood communities in valley bottoms and playas at 1500 to 1585 m in Juab and Millard (type from Desert Experimental Range) counties; Nevada; 10 (i). 2n = 18. The Bonneville saltbush is apparently a partially stabilized introgressant involving *A. gardneri* var. *falcata* and *A. canescens*. The habitat is intermediate between that of the parental taxa. There is evidence that the introgression is continuing in some populations at least.

Var. ***cuneata*** **(A. Nels.)** Welsh comb. nov. Castle Valley Saltbush. [based on: *Atriplex cuneata* A. Nels. Bot. Gaz. 34:357. 1902]. Saline, fine-textured substrates on Mancos

Shale, and other formations of similar texture and salinity, in greasewood and mat-atriplex communities at 1220 to 2170 m in Carbon, Duchesne, Emery (type from near Emery), Garfield, Grand, San Juan, and Uintah counties; Colorado and New Mexico; 166 (xxi). 2n = 18, 27, 36, and higher. A series of at least partially stabilized introgressants between var. *cuneata* and var. *tridentata* in Carbon County form the basis of *A. cuneata* ssp. *introgressa* C. A. Hanson. Possibly they warrant taxonomic recognition, but no nomenclatural combination is intended or implied herein.

Var. *falcata* (Jones) Welsh comb. nov. Jones Saltbush. [based on: *Atriplex nuttallii* var. *falcata* Jones Contr. W. Bot. 11:19. 1903]. Sagebrush, shadscale, and greasewood communities at 1310 to 1985 m in Box Elder, Iron, Juab, Millard, Rich, and Tooele counties; Washington to Montana, south to Nevada and Wyoming; 30 (i).

Var. *gardneri* Gardner Saltbush. Greasewood and sagebrush-saltbush communities at ca 1895 m in Daggett County; Wyoming, Colorado, and Montana; 6 (0).

Var. *tridentata* (Kuntze) Macbr. Basin Saltbush. [*A. tridentata* Kuntze; *A. nuttallii* var. *utahensis* Jones, type from Salt Lake City]. Greasewood, shadscale, alkali saccaton, kochia, saltgrass, and sedge-rush communities at 1280 to 1985 m in Beaver, Box Elder, Cache, Carbon, Davis, Duchesne, Iron, Juab, Millard, Piute, Salt Lake, Sanpete, Sevier, Tooele, and Uintah counties; Colorado, Nevada, Idaho, and Wyoming; 95 (iv). 2n = 18, 36, 54. Materials from eastern Utah have leaves narrower on the average than those from the Great Basin. The bracts are more heavily tuberculate also.

Var. *welshii* (C. A. Hanson) Welsh comb. nov. Welsh Saltbush. [based on: *Atriplex welshii* C. A. Hanson Studies Systematic Botany 1:1. 1962]. Mat-saltbush and Castle Valley saltbush communities at 1280 to 1315 m in Grand County; endemic; 10 (ii). 2n = 18.

***Atriplex garrettii* Rydb.** Garrett Saltbush [*A. canescens* ssp. *garrettii* (Rydb.) H. & C.; *A. canescens* var. *garrettii* (Rydb.) Benson]. Dioecious (rarely monoecious) shrubs or subshrubs, mainly 2–6 dm tall, unarmed; leaves opposite or subopposite below, petiolate, the blades 8–55 mm long, 6–32 mm wide, ovate to obovate, elliptic, or orbicular, yellow-green, sparingly scurfy, entire or repand-dentate, obtuse to cuneate basally, rounded to acute apically; staminate flowers brown to tan (rarely yellow), in clusters 2–4 mm wide on panicles 2–8 cm long; pistillate flowers in spikes or spicate panicles 4–30 cm long; fruiting bracts 6–10 mm long and wide, winged, the surface smooth, reticulate, or with flattened processes, toothed apically; seeds ca 2 mm wide, brown. 2n = 18. Shadscale, ephedra, eriogonum, blackbrush, and mixed shrub-grass communities on talus slopes of canyons of the Colorado at 1125 to 1895 m in Garfield, Grand (type from near Moab), Kane, San Juan, and Wayne counties; endemic; 41 (xii). 2n = 18. This distinctive plant has been regarded as a portion of the variation within an expanded *A. canescens*, with which it shares the feature of 4-winged pistillate fruiting bracts, but it is possibly more closely allied with *A. confertifolia*, with which it hybridizes.

***Atriplex graciliflora* Jones** Blue Valley Orach. Monoecious annual herbs, mainly 1–3 dm tall, branching from the base; leaves alternate, petiolate, the blades 8–10 mm long and about as wide or wider, cordate-ovate to orbicular, cordate, or deltoid, truncate to cordate basally, rounded to obtuse or acute apically, entire; staminate flowers in panicles overtopping the foliage, the perianth 5-lobed; pistillate flowers axillary; fruiting bracts samaralike, 6–16 mm wide, stipitate, compressed, orbicular, oblong or cordate in outline, winged, the wings undulate or entire, the surfaces smooth; seeds ca 3 mm wide, dull white. Saltbush, seepweed, greasewood, rabbitbrush, and tamarix communities on saline, often salt-encrusted, soils at 1125 to 1900 m in Carbon, Emery, Garfield, Kane, and Wayne (type from Blue Valley) counties; Colorado; 18 (iii).

***Atriplex heterosperma* Bunge** Two-seed Orach. Moenocious annual herbs, mainly 1.5–14 dm tall, erect, branched from below the middle or above; leaves opposite or subopposite below, commonly alternate above and petiolate, the blades mainly 15–80 mm long and as wide or wider, hastately lobed, triangular, the base truncate to cordate or obtuse, acute apically; staminate flowers with

5 sepals; fruiting bracts 2–7 mm long, orbicular to suborbicular or ovate, entire, the surfaces smooth, dimorphic, the larger with a pale brown vertical seed 2–3 mm wide, the smaller with a shiny black vertical seed ca 1 mm wide. 2n = 36. Riparian and palustrine (less commonly ruderal) habitats in greasewood, saltgrass, cocklebur, tamarix, cottonwood, and rush-cattail communities at 1310 to 1985 m in Box Elder, Cache, Davis, Duchesne, Emery, Juab, Salt Lake, Sanpete, Sevier, Summit, Uintah, and Weber counties; western North America; adventive from Eurasia; 29 (ii). This is a handsome vigorous annual that appears to be invading saline lowland and other disturbed areas throughout the state.

***Atriplex hortensis* L.** Garden Orach. Monoecious annual herbs, mainly 5–20 dm tall, erect, branching from the middle or above; leaves opposite or subopposite below, alternate above, petiolate, the blades commonly 1.5–13.5 cm long and 1–13 cm wide, ovate to lanceolate, not especially hastate, the base acute to cordate, acute to rounded apically; staminate flowers with 3–5 sepals; pistillate flowers dimorphic, the pistil vertical and enclosed in bracts or the pistil horizontal and enclosed in a 4- or 5-lobed calyx, both shortly pedicellate; fruiting bracts 8–19 mm long, orbicular to ovate, entire, the surfaces smooth, greenish or reddish; seeds dimorphic, either 2–4 mm wide and brown or ca 1 mm wide and black. Disturbed sites in riparian and ruderal habitats at 1310 to 2135 m in Cache, Duchesne, Salt Lake, Sanpete, Summit, Tooele, Uintah, and Utah counties; practically cosmopolitan, introduced from Eurasia; 12 (i). This plant is grown as a potherb, and is to be expected practically anywhere. It persists and escapes following cultivation.

***Atriplex hymenelytra* (Torr.) Wats.** Desert Holly. [*Obione hymenelytra* Torr.]. Dioecious shrubs, 3–15 dm tall or more, unarmed; leaves persistent, petiolate, alternate, the blades 10–40 mm long and as wide or wider, orbicular to reniform or oval, greenish to silvery white, permanently scurfy, prominently dentate; staminate flowers yellow to purple-brown, in clusters 3–4 mm thick, borne in panicles to 3 cm long; pistillate bracts subsessile, 7–10 mm long and wide, orbicular to reniform, the margins entire to crenate; seeds ca 2 mm wide, brown. Warm desert shrub community at ca 730 m in Washington County; Arizona, Nevada, California, and Mexico; 4 (0). This is a handsome rounded shrub with silvery white foliage. It flowers very early in springtime.

***Atriplex lentiformis* (Torr.) Wats.** Big Saltbush. [*Obione lentiformis* Torr. in Sitgr.]. Dioecious or, less commonly, monoecious shrubs, mainly 10–25 dm tall, unarmed; branchlets terete; leaves persistent, alternate, petiolate, the blades 0.5–4 cm long, 0.3–3 cm wide, deltoid to rhombic, ovate, or oblong-elliptic, gray-green, scurfy, entire to repand or subhastately lobed, rounded to obtuse apically; staminate flowers yellow, in clusters 1–2 mm wide, borne in panicles 0.5–5 dm long; fruiting bracts 3–4 mm long and wide, sessile, orbicular to oval, crenulate, rounded apically; seeds ca 1–1.5 mm wide, brown. Drainages, stream and canal banks, and roadsides in warm desert shrub communities at 760 to 950 m in Washington County; Arizona, Nevada, California, and Mexico; 8 (0).

***Atriplex obovata* Moq.** New Mexico Saltbush. Dioecious shrubs, mainly 2–8 dm tall; leaves tardily deciduous, alternate, shortly petiolate, the blades 8–30 mm long, 6–20 mm wide, obovate to elliptic or orbicular, gray-green, entire or rarely dentate, rounded to retuse or obtuse apically; staminate flowers yellow, in clusters 2–3 mm wide, borne in panicles 6–30 cm long; fruiting bracts 4–5 mm long, 5–9 mm wide, sessile, broadly cuneate, the surfaces smooth or rarely tubercled, the margins entire, the apical tooth subtended by 2–6 equal or smaller teeth; seeds 1–1.5 mm wide, brownish. Salt desert shrub and lower pinyon-juniper communities at ca 1525 to 1650 m in San Juan County; Arizona, New Mexico, and Mexico; 6 (i).

***Atriplex patula* L.** Fat-hen Saltbush. Monoecious annual herbs, mainly 1.5–10 dm tall, prostrate-ascending or erect, simple or branched; leaves alternate or some or all opposite, petiolate, the blades mainly 1–12 cm long, 1–5 cm wide or more, ovate, deltoid, lance-ovate, or lance-linear, cordate to hastate, truncate, or acute to cuneate basally, rounded to obtuse or acute apically, entire to dentate or hastate, thin or thick, green, glabrous or scurfy; flowers in paniculate clusters; staminate flowers with 4 or 5 sepals; fruiting bracts sessile, subsessile, or rarely stipitate, 2–12 mm long, 3–9 mm wide, deltoid to ovate or rhombic, sometimes spongy-thickened, the margin entire or denticulate, the face smooth, roughened, or tuberculate; seeds vertical, dimorphic, either black and 1–2 mm wide or brown and 1–3 mm wide. This species complex consists of plants with circumboreal representation. Our material apparently consists of introduced and indigenous portions of that complex, often treated at specific status or in various infraspecific categories. Treatment as a broad, highly variable taxon consisting of two infraspecific taxa seems to best represent our material. The following key will serve to segregate most specimens.

1. Principal lower leaves triangular-hastate; leaf bases truncate, broadly cuneate, or subcordate; plants common .... *A. patula* var. *triangularis*

— Principal lower leaves various, but seldom hastate; leaf bases acute to cuneate; plants uncommon .... *A. patula* var. *patula*

Var. *patula*. Sedge-reed, tamarix-Russian olive, and willow-cottonwood communities at 1370 to 1985 m in Rich, Sanpete, and Utah counties; widespread in North America; Eurasia; 3 (i). Materials tentatively assigned here are thin-leaved, but bracts vary in outline from rhombic to ovate or narrowly oblong and the surfaces from smooth to tubercled.

Var. *triangularis* (Willd.) Thorne & Welsh comb. nov. [based on: *Atriplex triangularis* Willd. Sp. Pl. 4:936. 1805; *A. hastata* authors, not L.; *Chenopodium subspicatum* Nutt.; *A. subspicata* (Nutt.) Rydb.; *A. carnosa* A. Nels.]. Saltgrass, sedge-rush, rush-cattail, and other palustrine and riparian habitats, usually in saline mucky soils at 850 to 1985 m in Cache, Davis, Duchesne, Emery, Millard, San Juan, Salt Lake, Sanpete, Uintah, and Washington counties; widely distributed in North America; Europe; 31 (v). Both thick and thin-leaved specimens are included in this variety. The problem of typification of *A. hastata* L. was reviewed by Taschereau (Canad. J. Bot. 50:1585, 1972). That name evidently replaces the long-established *A. calotheca* (Rafn.) Fr., a plant not known from Utah. The next available epithet at specific rank is apparently *A. triangularis* Willd., herein treated at varietal level. It seems likely that another name might well supersede that name at varietal rank.

Atriplex powellii Wats. Powell Orach. Dioecious (sparingly monoecious) annual herbs; stems slender to stout, mainly 1–5 (7) dm tall, branching almost throughout; herbage pubescent with scurfy and arachnoid hairs; leaves alternate, petiolate, or the upper sessile, the blades 0.4–5 cm long, 0.2–3 cm wide, ovate to rhombic or elliptic, entire, rounded to cuneate basally, acute to obtuse apically, prominently 3-veined; staminate flowers with calyx 4- or 5-lobed; fruiting bracts sessile, 2–2.8 mm long, 1.5–3.2 mm wide, thick, united to the apex, ovate to oblong or broadly cuneate, truncate to cuspidate apically, the surfaces with thickened processes or rarely smooth; seeds ca 2 mm long, greenish. Saline, usually fine-textured substrates, in greasewood, rabbitbrush, shadscale, seepweed, mat-atriplex, juniper-pinyon, and blackbrush communities at 1220 to 1830 m in Carbon, Duchesne, Emery, Garfield, Grand, Kane, Sanpete, Sevier, Tooele, Utah, and Wayne counties; Montana and South Dakota to Arizona and New Mexico; 54 (ix). This is the only annual atriplex in Utah that approaches being truly dioecious, but occasionally a few flowers of the opposite gender occur, resulting in sparingly monoecious individuals. The species in Utah is characteristic of the Colorado Drainage system. The few specimens from the Great Basin possibly represent recent introductions.

Atriplex rosei L. Tumbling Orach. Monoecious, coarse, annual herbs; stems simple or more commonly branching throughout, mainly 2–8 dm tall; herbage scurfy to glabrate; leaves alternate, petiolate, the blades mainly 1.2–7 cm long, 0.6–3.5 cm wide, ovate to lanceolate, acute to obtuse apically, irregularly dentate and often subhastately lobed; staminate flowers with 4 or 5 sepals; fruiting bracts sessile, 4–6 (8) mm long and as wide, ovate to rhomic, united to the middle, dentate, sharpely tuberculate on the surfaces; seeds dimorphic, brown and 2–2.5 mm wide, or black and 1–2 mm wide. Widely established weedy species of disturbed sites, often in riparian habitats or in barnyards or on animal bedgrounds, at 850 to 2560 m in all or nearly all Utah counties; widespread in North America; Eurasia and elsewhere; 47 (v).

Atriplex saccaria Wats. Stalked Orach. Low monoecious herbs, forming rounded clumps, mainly 0.5–2 (2.5) dm tall; stems usually branched from the base; herbage scurfy; leaves alternate or the lowermost subopposite, petiolate, the blades mainly 0.6–4 cm long, 0.4–3 cm wide, ovate to deltoid-ovate or oval, entire or in some the base subhastately lobed, truncate to subcordate or broadly cuneate basally, acute to rounded apically; staminate flowers with 5-parted perianth; fruiting bracts stipitate, or some subsessile to sessile, the faces smooth to coarsely tubercled or appendaged, mainly 4–6 mm long and as wide; seeds 2–3 mm wide, brownish to whitish. Two rather continuously intergrading varieties are present.

1. Pedicels of fruiting bracts 3–8 mm long or more, the bracts all essentially alike; plants uncommon .... *A. saccaria* var. *caput-medusae*
— Pedicels of fruiting bracts mainly less than 3 mm long, the bracts of lower axils tending to be subsessile and less tubercled than the upper ones .... *A. saccaria* var. *saccaria*

Var. *caput-medusae* (Eastw.) Welsh comb. nov. [based on: *Atriplex caput-medusae* Eastw. Proc. Calif. Acad. II. 6:316. 1896; *A. argentea* var. *caput-medusae* (Eastw.) Fosberg]. Medusa-head Orach. Greasewood, saltbush, and other salt-desert shrub communities at ca 1525 to 1600 m in Emery, San Juan (type from Recapture Creek), and Uintah counties; New Mexico and Arizona; 3 (i).

Var. *saccaria* [*A. cornuta* Jones, type from Green River]. Mat-atriplex, shadscale, greasewood, and pinyon-juniper communities at 1125 to 1830 m in Carbon, Daggett, Emery, Garfield, San Juan, Uintah, and Wayne counties; Wyoming to Arizona and New Mexico; 30 (vi).

***Atriplex semibaccata* R. Br.** Australia Saltbush. Decumbent, monoecious subshrubs, mainly 5–30 cm high and to 1 mm wide or more, unarmed; leaves alternate subsessile or shortly petiolate, mainly 0.8–3 cm long, 4–9 mm wide, obovate to oblong, remotely dentate, obtuse apically, attenuate basally, 1-veined; staminate flowers in clusters ca 1.5 mm wide; fruiting bracts sessile, 3–6 mm long and as wide, rhombic, united below, convex, red-fleshy at maturity, obtuse to acute apically, strongly veined; seeds dimorphic, ca 1.5 mm long and black, and ca 2 mm long and brown. Disturbed sites at ca 850 m in Washington County; southeastern U.S.; introduced from Australia; 5 (0).

***Atriplex torreyi* Wats.** Torrey Saltbush. Dioecious shrubs, mostly 8–30 dm tall, forming broad clumps; branchlets angled, becoming bluntly thorny; leaves alternate, persistent, with petioles 1–4 mm long, the blades 0.5–3 cm long, 4–16 mm wide, ovate to deltoid, rhombic, oval, or lanceolate, entire (rarely toothed), obtuse apically, truncate to obtuse basally; staminate flowers yellow, in clusters ca 1 mm wide, in panicles mainly 1–3 dm long; fruiting bracts sessile, 2–3 mm long and wide, orbicular, crenate, rounded apically; seeds ca 1–1.4 mm wide, brown. Mesquite, creosote bush, shadscale and blackbrush communities at ca 800 to 900 m in Washington County; Nevada and California; 13 (0).

***Atriplex truncata* (Torr.) Gray** Wedge Orach. [*Obione truncata* Torr. in Wats.; *A. subdecumbens* Jones, type from Fish Lake, Sevier County]. Monoecious annual herbs; stems simple or more commonly branched throughout, mainly 3–8 dm tall; herbage scurfy, becoming glabrate; leaves alternate, petiolate below, sessile above, the blades mainly 4–30 mm long, 3–30 mm wide, ovate to deltoid or oval, acute to obtuse apically, entire or dentate, truncate or subhastate to rounded basally; staminate flowers with 4 or 5 sepals; fruiting bracts sessile, 2–3 mm long and as wide, broadly cuneate, truncate apically, with 3 (or more) teeth across the summit, the surfaces smooth (rarely tubercled); seeds 1–2 mm wide, brown; 2n = 18. Saline saltgrass-greasewood and other palustrine habitats at ca 850 to 1375 (2700) m in Box Elder, Cache, Carbon, Emery, Juab, Millard, Rich, Salt Lake, Sevier, Utah, Washington, and Wayne counties; British Columbia to Montana, south to California and New Mexico; 12 (0).

Atriplex wolfii **Wats.** Slender Orach. [*A. tenuissima* A. Nels., type from Gunnison]. Monoecious, slender, delicate, annual herbs; stems simple or more commonly branched throughout, mainly 0.7–3.5 dm tall; herbage scurfy; leaves alternate, sessile, mainly 0.4–2.5 cm long, 1–3 mm wide, linear to narrowly lanceolate; staminate flowers with 5 sepals; fruiting bracts sessile, 1.5–3 mm long, 1–2.5 mm wide, ovate to cuneate in outline, truncate to attenuate apically, the faces smooth or tuberculate; seeds 1–2 mm long, brown. Greasewood community at 1525 to 2135 m in Carbon, Duchesne, Emery, Garfield, Piute, Sanpete, Sevier, and Uintah counties; Wyoming and Colorado; 7 (ii).

BASSIA All.

Annual herbs; leaves alternate, entire, sessile; herbage pilose or tomentose, at least in inflorescence; flowers perfect and pistillate, glomerate or solitary in leaf axils and in short axillary spikes, bracteate; calyx 5-lobed, depressed-globose, enclosing the fruit and usually prominently armed with a curved or hooked spine on the dorsal surface of each lobe; stamens 5, hypogynous; styles 1, with 2 (3) stigmas; fruit compressed; seed horizontal.

Bassia hyssopifolia **(Pallas) Kuntze** [*Salsola hyssopifolia* Pallas; *Echinopsilon hyssopifolius* (Pallas) Moq. in DC.; *Kochia hyssopifolia* (Pallas) Schrad.]. Annual herbs, the main stem erect, the lower lateral ones often decumbent, 2–10 dm tall; herbage more or less lanate, especially in inflorescence; leaves 4–40 mm long, 1–5 mm wide, linear to oblong narrowly oblanceolate; flowers clustered in terminal or lateral spikes, or solitary in leaf axils; floral bracts reduced; pistillate and sterile flowers mixed with perfect ones; fruiting calyx ca 2 mm wide, each lobe with a stout curved to uncinate spine; pericarp membranous, planoconvex. Commonly on saline substrates, often in riparian or palustrine habitats, in saltgrass, greasewood, horsebrush, shadscale, and cottonwood-tamarix communities at 850 to 2380 m in most, if not all, Utah counties; adventive from Eurasia; 34 (vii). This species forms apparent intergeneric hybrids with *Kochia scoparia*, from which *Bassia* differs in having spines on the sepals instead of horizontal flattened processes, inter alia.

BETA L.

Glabrous annual or biennial herbs; leaves alternate, petiolate, essentially entire; flowers perfect, solitary or borne in few-flowered cymes, these arranged in spicate terminal or axillary spikes; sepals 5; stamens 5; ovary partially inferior, connate with receptacle in fruit; stigmas 2 or 3; fruits adhering, fused by the swollen perianth and receptacle; seeds horizontal.

Beta vulgaris **L.** Stems mainly 4–10 dm tall or more; basal leaves well developed, long-petiolate, the blades mainly 5–25 cm long, 2–10 cm wide, undulate-crisped; inflorescence elongate, with lower bracts prominent; sepals incurved in fruit. Cultivated food plant, occasionally escaping but not persisting, mainly below 2135 m in much of Utah; introduced from Europe; 7 (0). This is the beet of commerce, including the red table beet and sugar beet. The latter was a major cash crop in Utah until the 1960s. Swiss chard, grown for use as a potherb, is a cultivar of this species.

CERATOIDES Gagnebin

Monoecious tomentose shrubs; leaves alternate, entire; staminate flowers ebracteate, with calyx 4-lobed; stamens 4; pistillate flowers lacking a perianth, enclosed in 2 villous-pilose, partially connate bracteoles, the tips divergent and hornlike; styles 2, slender; pericarp thin, free from the seed. [*Eurotia* Adans.; *Krascheninnikovia* Gueldenstaedt].

HOWELL, J. T. A new name for winterfat. Wasmann J. Biol. 29:105. 1971.

Ceratoides lanata **(Pursh) J. T. Howell** Winterfat; White-sage. [*Diotis lanata* Pursh; *Eurotia lanata* (Pursh) Moq.]. Shrubs, woody for 0.2–8 dm above ground (or more), and with numerous annual branchlets mainly 0.5–3 (5) dm long; herbage stellate-hairy, commonly with longer straight hairs intermixed, the hairs white or becoming yellowish in age; leaves 1–4.5 cm long, 1–6.5 mm wide, linear to narrowly lanceolate, entire, revolute to almost flat, sessile above, short-petiolate below; flowers borne in dense axillary clusters or more or less spicate along branch tips; pistillate flowers 2–4 per axil; staminate flowers in spicate axillary clusters, the perianth segments 1.5–2 mm long; fruiting bracts 3–6 mm long, obscured by the long covering hair. Shadscale, black sagebrush, sagebrush, bullgrass, sagebrush, and pinyon-juniper communities at 730 to 2840 m, known in all Utah counties except Salt Lake, Summit, Davis, Morgan, and Weber; Yukon to Saskatchewan, south to California, New Mexico, and Texas; 105 (ix). Three weakly differentiated morphological phases of winterfat are present in Utah. The common and most widely distributed phase (var. ***lanata***) is woody only at the base, has erect annual growth, and is moderately long-hairy as well as stellate. In Washington County and to a lesser extent in Kane County (mainly along Lake Powell) is a definitely woody plant with divaricate branches, which tend to persist as blunt thorns. The pubescence consists of a preponderance of stellate hairs, with few or none of the long slender ones being present. These plants are known as var. ***subspinosa*** **(Rydb.) J. T. Howell** [*Eurotia subspinosa* Rydb., type from Washington County]. A third phase is present in Grand and San Juan counties, where it grows in sandy parks surrounded by monoliths. The stems are woody for a distance of up to 8 dm or more, but the branching or current annual growth is erect as in var. *lanata* and the pubescence is intermediate between that of var. *subspinosa* and var. *lanata*. This latter plant is here designated as var. ***ruinina*** **Welsh** var. nov. Similis *Ceratoides lanata* var. *lanata* in ordinatem ramifacatem sed caulibus lignosis usque ad 8 dm altis et pubescentibus longis paucioribus differt. TYPE.— USA. Utah. San Juan County; T32S, R18E, S13, Beef Basin, Ruin Park, 2013 m elev., parkland in pinyon-juniper community on sand alluvium, 2 August 1983, S. L. Welsh & B. T. Welsh 22377 (Holotype BRY; isotypes NY; US; CAS; POM). Additional specimens: Utah. San Juan County; Chesler Park, T31S, R19E, S5, Sandy rolling grassland, fringed with juniper and pinyon, 1708 m elev., 14 Sept. 1964, S. L. Welsh, G. Moore, & M. Olsen 3730 (BRY); do, ca 15 mi SE of La Sal Jct., along power transmission line, sandy soil, Bouteloua grassland, 30 June 1970, L. C. Higgins 3550 (BRY). Grand County; Landscape Arch, Arches National Monument, 28 Sept. 1963, S. L. Welsh & G. Moore 2763 (BRY); do, near trail to Sand Dune Arch and Broken Arch, Arches National Park, 14 July 1972, J. S. Allan 130 (BRY). This variety, named for Ruin Park, is a striking phase of the species, with individuals in the populations exceedin 12 dm in height. All phases are considered as valuable browse plants for livestock, especially for sheep.

CHENOPODIUM L.

Annual herbs, glabrous, pubescent, glandular, or farinose (mealy); leaves alternate, flat, entire, toothed, or lobed; flowers perfect or some pistillate only, ebracteate, usually in cymes, variously arranged in spicate or paniculate inflorescences; calyx segments usually 4 or 5, persistent, flat or keeled, more or less covering the fruit, rarely becoming fleshy; stamens commonly 5; styles 2 (3); seeds lenticular, horizontal or vertical. Note: The genus is notoriously complex for several reasons. The floral features are greatly reduced and diagnostic characteristics are often based on either vegetative structures or on minutae of calyx, pericarp, and seed coat, which are often subject to interpretation and might be demonstrated ultimately as trivial. Nomenclature is tangled both within the native and introduced entities, leading to taxonomic treatments that do not satisfactorily represent the taxa as represented by actual specimens. Further, there is variability within the diagnostic features leading to contradictory statments in taxonomic treatments, e. g., with regard to such characters as adherent versus nonadherent pericarps. Thus, the treatment presented below attempts to provide names for the taxa recognizable in Utah based on examination of actual specimens. The entities seem to be real, but the names might be misapplied in some cases.

BASSETT, I.J. AND C. W. CROMPTON. 1982. The genus *Chenopodium* in Canada. Canad. J. Bot. 60:586–610.

WAHL, H. A. 1954. A preliminary study of the genus *Chenopodium* in North America. Bartonia 27:1–46.

1. Plants with yellow glands or glandular hairs, not farinose, aromatic 2

— Plants glabrous or farinose, eglandular, not aromatic 3

2(1). Flowers solitary in small cymes, these spreading-recurved along the axis of an elongate panicle; plants common .... *C. botrys*

— Flowers in small sessile clusters, borne in bracteate panicles; plants rare *C. ambrosioides*

3(1). Seeds all, or at least some, vertical in the flowers (except sometimes in C. glaucum, keyed both ways) 4

— Seeds usually all horizontal 6

4(3). Leaves mainly 0.5–2 cm long, 2–7 mm wide, irregulary dentate, glaucous-farinose beneath .... *C. glaucum*

— Leaves mainly larger and often hastately lobed, green or reddish beneath 5

5(4). Flowers in elongate axillary clusters, these forming erect or steeply ascending compact panicles; plants commonly palustrine .... *C. rubrum*

— Flowers in subglobose axillary clusters, these forming bracteate spikes; plants usually montane .... *C. capitatum*

6(3). Leaves 0.5–2 mm long, 2–7 mm wide, sinuate-dentate, glaucous-farinose beneath .... *C. glaucum*

— Leaves various, but not simultaneously as above 7

7(6). Larger cauline leaves more or less cordate to truncate basally, often over 4 cm wide, glabrous; sepals not keeled dorsally; panicles large and open .... *C. hybridum*

— Larger cauline leaves with bases various, but seldom as above, and less than 4 cm wide, often farinose beneath; sepals usually keeled 8

8(7). Larger cauline leaf blades mainly 3–5 or more times longer than wide, entire or with a pair of basal lobes 9

— Larger cauline leaf blades mainly 1–3 times longer than broad, hastately lobed, toothed, or entire 10

9(8). Leaves 1-veined, linear, entire; pericarp adherent to the seed .... *C. leptophyllum*

— Leaves 3-veined (at least near the base in larger ones), entire or with 2 basal lobes; pericarp not adherent to the seed .... *C. dessicatum*

10(8). Leaf blades hastately lobed (the lobe sometimes again lobed or toothed), or oval to elliptic and entire, or rarely with one or more teeth on the apical larger lobe; calyx lobes obscurely or narrowly membranous-margined; plants indigenous 11

— Leaf blades sinuate dentate, ovate to lanceolate, or entire; calyx lobes with broad scarious margins; plants adventive 12

11(10). Leaf blades not hastately lobed; pericarp usually adherent; plants usually of upper middle to higher elevations .... *C. atrovirens*

— Leaf blades often hastately lobed; pericarp not adherent; plants of wide altitudinal range .... *C. fremontii*

12(10). Fruits sharply angled on the margin; seed coat with minute rounded pits; plants uncommon in Washington and Sevier counties .... *C. murale*

— Fruits rounded to obtuse on the margin; seed coat smooth to sculptured; plants common or uncommon, of various distribution .... *C. album*

Chenopodium album **L.** Lambsquarter; pigweed. Erect annual herbs, the stems red-striate, 1–10 dm tall or more, simple or more commonly branched; herbage more or less farinose, at least when young; leaves petiolate, the blades 1–6.5 cm long, 0.5–5.6 cm wide, ovate to rhombic-ovate or lanceolate, sinuate-dentate and often subhastately lobed or the upper (rarely all) entire; flowers in dense glomerules, these spicate in upper axils; calyx with keeled lobes, enclosing the fruit; pericarp adherent; seeds horizontal, rounded marginally, smooth to sculptured, black, 1–1.5 mm wide. Two phases are present, which have been given taxonomic recognition.

1. Seeds sculptured, alveolate-reticulate, or reticulate .... *C. album* var. *berlandieri*
— Seeds smooth or faintly striate .... *C. album* var. *album*

Var. *album* Weedy species of disturbed habitats at 850 to 2265 m, probably in all Utah counties; widespread in North America; adventive from Eurasia; 53 (v). N = 27. This taxon has been confused with *C. fremontii*, q.v., but in those plants having mature fruits the adherent pericarps are diagnostic.

Var. *berlandieri* (Moq.) Mack. & Bush [*C. berlandieri* Moq.; *C. berlandieri* ssp. *zschackei* (Murr.) Zobel; *C. zschackei* Murr.] Weedy or pioneer plants of disturbed substrates in several plant communities at 1280 to 2585 m in Duchesne, Grand, Juab, Millard, San Juan, Sevier, and Utah counties; widespread in North America; 8 (v). N = 18. The speciman from Utah county (Welsh 3798 BRY) has the fruit nonadherent.

Chenopodium ambrosioides **L.** Mexican-tea. Aromatic annual herbs; stems erect or ascending, mainly 4–10 dm tall; herbage pubescent and with sessile glands; leaves short-petioled, the blades 2–10 cm long, 3–30 mm wide (or more?), usually lanceolate, dentate to laciniate; inflorescence paniculate, the cymes sessile on ultimate branches, usually bracteate; calyx united to the middle or above; seeds 0.5–0.8 mm wide. Ruderal and garden weeds of Utah and Washington counties; widespread in tropical and temperate New World; adventive from Mexico; 2 (0).

Chenopodium atrovirens **Rydb.** Mountain Goosefoot. [*C. fremontii* var. *atrovirens* (Rydb.) Fosberg; *C. hians* Standl.; *C. incognitum* Wahl]. Plants mainly 2–75 cm tall, the stems erect or steeply ascending, usually branched; herbage sparingly scurfy to glabrous; leaves petiolate, the blades 0.6–4 cm long, 2–23 mm wide, lanceolate to ovate, entire or obscurely hastately lobed, otherwise entire, obtuse basally; flowers clustered in leaf axils or in interrupted terminal spikes, the lower ones subtended by foliose bracts, becoming ebracteate upward; perianth lobes free to below the middle, keeled dorsally; pericarp adherent or, less commonly, not adherent to the horizontal rugulose to smooth, obtusely margined seed; seeds ca 0.9–1.3 (1.5) mm wide. 2n = 18. Sagebrush, pinyon-juniper, mountain brush, ponderosa pine, Douglas fir, aspen-tall forb, and spruce-fir communities at 1705 to 3175 m in Beaver, Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Rich, Salt Lake, Sanpete, Sevier, Summit, Utah, and Wasatch counties; British Columbia to Saskatchewan, south to California, Nevada, Colorado, and Iowa; 24 (ii). Relationship of this species probably lies closer to the *leptophyllum* end of the spectrum. The occasional specimens with free pericarps might indicate intermediacy with *C. fremontii*, however. There has been little agreement between previous authors as to whether the pericarp was adherent or not, but in the specimens examined from Utah, the pericarps are usually adherent.

Chenopodium botrys **L.** Jerusalem-oak. Aromatic annual herbs; stems commonly 1–5 dm tall, erect or ascending, usually branched; herbage glandular-villous; leaves petiolate, the blades sinuate-pinnatifid, the lobes again toothed or lobed, oblong to oval in outline; inflorescence an erect panicle of loosely spreading-recurved cymes, mainly shortly bracteate; sepals ca 1 mm long; seeds horizontal or vertical, 0.5–0.8 mm wide, dull, dark. 2n = 18. Widespread ruderal weedy species, established locally in indigenous communities, especially in gravelly washes at 760 to 1985 m in Beaver, Cache, Iron, Juab, Millard, Salt Lake, Sevier, Utah, and Washington counties; widely distributed in the U.S.; adventive from Eurasia; 22 (iii).

Chenopodium capitatum (L.) Asch. Strawberry-spinach. [*Blitum capitatum* L.; *C. overi* Aellen in Fedde?; *C. chenopodioides* authors, not (L.) Aellen]. Plants mainly 1–4 dm tall, the stems erect or decumbent-ascending, simple or more commonly branched from the base; herbage glabrous; leaves petiolate, the blades (1) 1.5–10 cm long, 1–10 cm wide, triangular-hastate to lanceolate, shallowly to deeply toothed or subentire, hastately lobed or the upper entire, acute to obtuse apically, often turning reddish; flowers clustered in axillary capitate spikes, the lower clusters subtended by foliose bracts, the upper ones ebracteate or with reduced bracts; perianth lobes free to below the middle, not mealy, becoming fleshy and reddish, shorter than the fruit; pericarp adherent to the erect (or less commonly horizontal) seed; fruit ca 1 mm long. 2n = 18. Two varieties are present in Utah.

1. Flower clusters often over 5 mm wide, the calyx becoming red and fleshy at maturity; plants uncommon .... *C. capitatum* var. *capitatum*
— Flower clusters commonly less than 5 mm wide, the calyx not fleshy, though sometimes reddish at maturity; plants common ...... *C. capitatum* var. *parvicapitatum*

Var. ***capitatum*** Gravelly soil in lodgepole pine forest, north slope of Uinta Mts. (Welsh & Moore 6696 BRY), Summit County; Alaska to Quebec, south to California, New Mexico, and New England; 1 (i).

Var. ***parvicapitatum*** **Welsh var. nov.** Similis *Chenopodio capitato* var. *capitato* sed in capitulis parvioribus et calycibus ecarnosis differt. Type: USA. Utah. Beaver County; T27S, R6W, S35, Fish Lake Forest, Tushar Mountains, Indian Creek, ca 12 mi due NE of Beaver, 2288 m, mixed conifer-aspen streamside forest, igneous gravel, 28 June 1978, S. L. Welsh, M. Welsh, & E. Welsh 17148 (Holotype BRY; Isotypes seven, distributed previously as *C. rubrum* L.). Additional specimens: Utah. Garfield County; pass between Table Cliff Plateau and Escalante Mts., Beck & Tanner sn (BRY). Millard County; Canyon Mts., 6 mi SSW of Scipio, 11 June 1980, S. Goodrich 13993 (BRY). Grand County; ca 19 mi NNE of Thompson, Middle Willow Creek, 9 August 1977, S. Welsh & S. White 15853 (BRY). Summit County; Soapstone, 12 July 1928, W. P. Cottam 3779 (BRY). Wasatch County; Strawberry Valley, Mud Creek, 30 July 1964, V. B. Matthews 123 (BRY). Utah County; Mt. Timpanogos, Timpanogos Lodge area, 13 June 1974, K. Allred 854 (BRY). Mountain brush, ponderosa pine, aspen, and spruce-fir communities at 1860 to 3050 m in Beaver, Cache, Carbon, Daggett, Duchesne, Garfield, Grand, Iron, Juab, Kane, Millard, Salt Lake, Sanpete, Summit, Tooele, Uintah, and Utah counties; British Columbia to Saskatchewan, south to California, Nevada, and Colorado; 60 (xiv). This common plant of montane habitats has been identified variously as *C. capitatum* or *C. rubrum*, and, more recently, as *C. chenopodioides* (L.) Aellen. The latter plant is a portion of the flora of the Soviet Union and might represent nothing more than phases of *C. rubrum* sensu lato. Certainly the description provided for that entity (Flora SSSR 6:51.1936) is not of our specimens, and neither is the habitat cited (i.e., "wet solonchaks"). The name given here is for the purpose of providing an unequivocal epithet for this montane western American phase of *C. capitatum*.

Chenopodium dessicatum **A. Nels.** Desert Goosefoot. [*C. pratericola* Rydb.; *C. petiolare* var. *leptophylloides* Murr.; *C. leptophyllum* var. *dessicatum* (A. Nels.) Aellen; *C. leptophyllum* var. *oblongifolium* Wats.; *C. pratericola* var. *oblongifolium* (Wats.) Wahl]. Plants mainly 3–8 dm tall, the stems erect, simple or branched; herbage commonly more or less scurfy; leaves petiolate, the blades mostly 1.3–6 cm long and 2–10 (15) mm wide, linear to narrowly lanceolate or elliptic, entire or less commonly hastately lobed, cuneate basally; flowers clustered in terminal or axillary spicate panicles; perianth lobes free to below the middle, keeled dorsally; pericarp not adherent to the horizontal smooth to rugulose, obtusely margined seed; seeds 0.9–1.2 mm wide. 2n = 18. Shadscale, hopsage, rabbitbrush, tamarix-poplar, sagebrush, and pinyon-juniper communities at 850 to 1925 m in

Duchesne, Emery, Garfield, Grand, Kane, Salt Lake, San Juan, Uintah, Utah, Washington, and Wayne counties; Yukon to Manitoba, south to California, New Mexico, and Nebraska; 26 (iii). Material assigned to *C. dessicatum* in a strict sense, as distinct from *C. pratericola* in a strict sense, has perianth lobes covering the mature fruit, as opposed to having the fruit not covered. The distinction is not great. Reduction of this taxon to *C. leptophyllum* (as var. *oblongifolium*) begs the question of a probably nearer relationship to *C. fremontii*, with which it shares nonadherent pericarp and broader, more veined leaves. Furthermore, apparent intermediates between *C. fremontii* and *C. dessicatum* exist. The entire complex is in need of monographic study.

Chenopodium fremontii **Wats.** Fremont Goosefoot. Plants mainly 1–8 (12) dm tall, the stems erect or ascending, usually branched; herbage more or less scurfy to glabrous; leaves petiolate, the blades 0.6–5 (6) cm long, and about as broad, less commonly 2–3 times longer than broad, triangular-ovate to ovate or lanceolate, commonly hastately lobed, the lobes often again lobed or toothed, otherwise entire or rarely with 1 or few teeth on the main apical lobe, broadly cuneate to subcordate basally; flowers clustered in large terminal and smaller lateral spikes, scurfy; perianth lobes free to below the middle, keeled dorsally; pericarp not adherent to the horizontal, smooth to rugulose, obtusely margined seed; seeds 0.9–1.2 mm wide. N = 9. This closely interrelated complex of forms involves the linear-leaved *C. leptophyllum* (q.v.) at one end of the spectrum and the broad-leaved phases of *C. fremontii* at the other end (and with both *C. atrovirens* and *C. dessicatum*, inter alia, be tween the extremes). The intervening plants have been regarded as species or some of them have been placed within expanded species concepts at both ends of the series. The course followed herein is a compromise between having one all-inclusive species, with numerous varieties, and that of recognition of all of the named entities at specific level. The proposed treatment attempts to represent the major taxa as they occur in Utah; the synonymy might not be properly applied in all cases.

1. Plants mainly less than 25 cm tall, branching from the base, the curved ascending branches subequal to the main stem; leaves more or less white-farinose, at least beneath .... *C. fremontii* var. *incanum*

— Plants 0.5–8 dm tall, variously branched, but if as above, the lateral branches much shorter than the main stem; leaves white- farinose to glabrous .... *C. fremontii* var. *fremontii*

Var. ***incanum*** **Wats.** [*C. incanum* (Wats.) Heller; *C. watsonii* of authors, not A. Nels.?]. Blackbrush, salt desert shrub, pinyon-juniper, mountain brush, and ponderosa pine communities at 850 to 2350 m in Carbon, Duchesne, Emery, Garfield, Juab, Kane, Piute, Salt Lake, Tooele, Uintah, Wayne, and Washington counties; Nevada to Nebraska, south to Texas and Mexico; 28 (iii). The variety is transitional to the next.

Var. ***fremontii*** Blackbrush (and other warm desert shrub), salt desert shrub, sagebrush, mountain brush, pinyon-juniper, aspen, and spruce-fir communities at 850 to 3050 m in Beaver, Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Juab, Piute, Salt Lake, San Juan, Sevier, Summit, Tooele, Uintah, Utah, Washington, Wayne, and Weber counties; British Columbia to Manitoba, south to California and Mexico; 63 (xix). Specimens assigned here are not uniform with regard to leaf shape, plant height, and openness of the inflorescence. More work is indicated.

Chenopodium glaucum **L.** Oakleaf Goosefoot. [*C. salinum* Standl.]. Plants mainly 3–30 cm long, the stems prostrate to ascending or erect, usually branched; herbage farinose, especially on lower leaf surfaces; leaves shortly petiolate, the blades 4–25 mm long, 2–10 mm wide, lanceolate to oblong or ovate, coarsely sinuate-dentate; flowers in clusters in numerous short, bracteate or ebracteate, axillary spikes and a terminal spicate panicle; perianth cleft almost to base, not enclosing the fruit; pericarp not adherent to the seed; seeds horizontal or vertical, 0.8–1.3 mm wide, smooth. N = 9. Often in saline substrates on lake shores and stream banks, in sedge-rush, tamarix-sedge, rabbitbrush, pinyon-juniper, and aspen to spruce-fir communities at 1220 to 2745 m in Cache, Carbon, Duchesne, Garfield, Grand, Kane, Millard, Salt Lake, Sanpete, Sevier, Uintah, Utah, and Wayne counties; widespread in U.S. and Canada; Eurasia; 26 (xiv). Our material is assignable to var. ***salinum*** **(Standl.) B. Boi.**, on the basis of its larger fruits (0.8–1.3 mm, not 0.6–0.9 mm).

Chenopodium hybridum **L.** Mapleleaf Goosefoot. [*C. gigantospermum* Aellen]. Plants mainly 2–10 dm tall, the stems erect, simple or branched; herbage glabrous, except in inflorescence; leaves alternate or the lower often opposite, long petiolate, the blades commonly 1.7–10 cm long, 1.2–10 cm wide, ovate to deltoid ovate, sinuate-dentate to -lobate, with 2–4 teeth or lobes, cordate to truncate or obtuse basally; flowers in small cymes, these arranged in large terminal and smaller axillary panicles, more or less farinose and often sparingly glandular; perianth cleft nearly to the base, not strongly keeled dorsally; pericarp not or moderately adherent; seeds 1.2–1.9 mm wide, with obtuse margin, smooth or somewhat sculptured. $2n=18$. Sagebrush, pinyon-juniper, mountain brush, ponderosa pine, and aspen communities, less commonly in riparian or palustrine habitats, at 1280 to 2135 m in Beaver, Cache, Millard, Salt Lake, Sanpete, Summit, Tooele, Utah, and Weber counties; widely distributed in U.S. and Canada; Europe; 12 (iv). Our specimens have been identified as **var. *gigantospermum*** **(Aellen) Rouleau,** on the basis of the seed being less sculptured than in typical European material. Plants of this species formed huge stands in burned over sagebrush and aspen communities in Summit County in 1963.

Chenopodium leptophyllum **(Moq.) Wats.** Narrowleaf Goosefoot. [*C. album* var. *leptophyllum* Moq.]. Plants mainly 12–70 cm tall, erect or the branches ascending, simple or branched; leaves short-petiolate, the blades mainly 0.7–4 cm long, 1–5 (7) mm wide, linear to narrowly oblong or narrowly lanceolate, 1-veined, cuneate to acute basally, entire; flowers in loose to compact cymes aggregated into terminal or axillary spicate panicles; perianth lobes cleft to well below the middle, keeled dorsally; pericarp adherent; seeds horizontal, 0.9–1.1 mm wide, black, finely rugulose to smooth. $2n=18$. Shadscale, greasewood, rabbitbrush, tamarix, sagebrush, fringed sagebrush, mountain brush, and aspen communities at 1125 to 2900 m in Cache (?), Carbon, Daggett, Duchesne, Garfield, Grand, Piute, Salt Lake, San Juan, Summit, Tooele, Uintah, and Wayne counties; British Columbia to Saskatchewan, south to California and Mexico; 34 (xiii). The 1-veined, narrow leaf blades and adherent pericarps are apparently definitive for this plant.

Chenopodium murale **L.** Nettleleaf Goosefoot. Plants mainly 2–5 dm tall, the stems erect or with branches ascending; herbage glabrous or sparingly farinose, especially in inflorescences; leaves petiolate, the blades 1–5 (7) cm long and as broad or nearly so, ovate to oval or lanceolate, irregularly sinuate-dentate and some often subhastate, cuneate to subcordate basally; flowers sessile and solitary to clustered in axillary or terminal panicles not much, if at all, surpassing the leaves; perianth lobes free to below the middle, keeled dorsally; pericarp adherent to the horizontal, rugulose to smooth, sharply margined seed; seeds 1–1.5 mm long. $2n=18$. Ruderal weeds at 730 to 1620 m in Sevier and Washington counties; widespread in U.S. and Canada; adventive from Eurasia; 5 (0).

Chenopodium rubrum **L.** Red Goosefoot. Plants mainly 0.5–10 dm tall, erect, simple or with steeply ascending branches; herbage glabrous or somewhat villous in inflorescence; leaves petiolate, the blades 0.7–9 cm long, 0.4–7 cm wide, trianglular to ovate, lanceolate, or elliptic, sinuate-dentate or -lobed, some often subhastate, fleshy and often suffused with red; flowers sessile, the clusters borne in simple or branched axillary and terminal spicate panicles; perianth lobes cleft to the middle or below, rounded or sometimes keeled dorsally; pericarp not adherent; seeds nearly always vertical, oval in outline, 0.7–1 mm long. $2n=18$. Saline moist substrates in palustrine and riparian habitats at 1280 to 2440 m in Box Elder, Cache, Daggett, Duchesne, Salt Lake, Uintah, and Utah counties; widespread in U.S. and Canada; Eurasia; 18 (i).

CORISPERMUM L.

Annual herbs, often pubescent with stellate hairs; leaves alternate, sessile, entire, 1-veined; flowers perfect, solitary or clustered in bract axils, arranged in dense or lax spikes; perianth segments 1–3, minute, unequal, the posterior one largest, erect, 1-nerved, scarious; stamens 1–3 (5); stigmas 2, connate basally; achenes strongly flattened, plano-convex, indurate, the margin winged or acute.

Corispermum villosum **Rydb.** Bugseed; tickseed. [*C. hyssopifolium* authors, not L.; *C. nitidum* authors, not Kit in Schult.; *C. imbricatum* A. Nels.; *C. emarginatum* Rydb.; *C. marginale* Rydb.; *C. simplicissimum* Lunnel?]. Stems mainly 8–50 cm tall, commonly branched throughout, the lower branches often curved-ascending to ascending, usually reddish; herbage glabrous or sparsely to densely pubescent with soft, branched hairs; leaves alternate, sessile, semicylindric and more or less involute or subulate, mostly 0.8–6 cm long, 0.5–3 mm wide, apiculate; inflorescence slender and elongate or compact, the bracts broadly scarious-margined, with the lower ones narrower or broader than the fruit, the upper ones usually broader than the fruit; perianth mostly consisting of a single posterior erose segment (rarely with 2 additional small anterior-lateral segments); stamens 3–5; fruit 2.2–4.1 mm long, 1.6–2.6 mm wide, oval to suborbicular, smooth, glabrous, brownish; wings opaque, stramineus, one-eighth to one-fifth as wide as the body. Usually in sand, in ephedra, four-wing saltbush, rabbitbrush, scurfpea, and pinyon-juniper communities, at 1065 to 1955 m in Duchesne, Garfield, Grand, Juab, Kane, Millard, San Juan, Uintah, and Wayne counties; Montana and North Dakota, south to Arizona, New Mexico, and Texas; 20 (iv). Our specimens have long been presumed to be introduced and conspecific with either *C. hyssopifolium* L. and/or *C. nitidum* Kit. in Schult. While the details of those taxa are reported in contradictory fashion in Flora SSSR (6:146–149. 1936) versus the Flora Europaea (1:99–100. 1964), it seems clear that our plants cannot be *C. hyssopifolium*, which is reported to have flat leaves. The description of our specimens more nearly fits that of *C. nitidum*, but that plant has filiform leaves, not semicylindric ones as in ours. Further, our plants grow in native plant communities and are not weedy; their distribution pattern is that of numerous other indigenous taxa. Plants of this genus were described historically from the edge of civilization and beyond in North America (Nuttall, Genera of North American Plants 1:4. 1818; Hooker, Flora Boreale Americana 2:126. 1838; Watson, Proc. Amer. Acad. 9:123. 1874). Although not definitive evidence of nativity, these historical data add to the weight of evidence for the indigenous nature of the genus in North America. Because of these considerations I have, arbitrarily, chosen the earliest name available at specific level for our plants. Both elongate slender and short broad inflorescences are represented within our specimens, along with occasional intermediates. There is little correlatation of inflorescence type with other morphological features or geography.

Cycloloma Moq.

Annual herbs; stems commonly branched and forming rounded clumps; leaves alternate, sinuate-dentate; herbage more or less pubescent, eglandular; inflorescence a panicle of interrupted spikes; flowers sessile; perianth 5-lobed, the segments in fruit with a transverse wing on the back, the wings connate and completely encircling the fruit; stamens 5; achenes depressed; seeds horizontal.

Cycloloma atriplicifolia **(Spreng.) Coult.** Winged-pigweed. [*Salsola atriplicifolia* Spreng.]. Plants mainly 0.8–5 dm tall (rarely more), divaricately branched, the stems striate, loosely and sparingly tomentulous, becoming glabrate; leaves short petioled to sessile, the blades 1–8 cm long, 2–15 mm wide, coarsely serrate-dentate, acute apically, cuneate basally; flowers perfect and pistillate; sepals 5, keeled, the perianth developing into a horizontal wing; wings white-hyaline, lobed or toothed, 4–5 mm in diameter, often red or purple at maturity; ovary tomentulose; styles 2 or 3; fruit enclosed in calyx; seed ca 1.5 mm wide, black, smooth; pericarp not adherent. Sandy habitats in blackbrush, mixed desert shrub, and juniper communities at ca 1125 to 1465 m in Garfield, Grand, Kane, San Juan, and Wayne counties; Manitoba and Indiana, south to Arizona and Texas; adventive in Europe; 10 (iii).

GRAYIA H. & A.

Dioecious or less commonly monoecious shrubs or subshrubs; branches more or less thorny; axillary buds subglobose, prominent; leaves alternate, entire; herbage or pubescent with simple or stellate hairs; flowers in terminal and axillary spicate panicles, imperfect; staminate flowers 2–5 in clusters in bract axils, not separately bracteolate, the perianth 4- or 5-lobed, subequal to the 4 or 5 stamens; pistillate flowers 1-several per bract, often some vestigial, each enclosed by 2 connate bracteoles, the more or less accrescent bracteoles obcompressed, the margins thickened and spongy within; fruits vertical; stigmas 2.

Grayia spinosa **(Hook.) Moq.** Hopsage. [*Chenopodium (?) spinosum* Hook.; *G. polygaloides* H. & A.]. Shrubs, mainly 5–12 (15) dm tall; branches gray brown; branchlets with bark exfoliating in long strips; pubescent with scurfy and stellate hairs when young, often spinose-persistent; leaves 5–30 mm long (or more), mainly 2–12 mm wide, spatulate to oblanceolate, entire, tapering to a short petiole; staminate flowers with usually 4-lobed perianth, enclosing the 4 stamens, 1.5–2 mm long; pistillate flowers in short spicate inflorescences, the subtending bracts reduced, enclosed by paired, accrescent, obcompressed bracts, orbicular or cordate, the wings thickened and spongy within, 6–15 mm wide, greenish, straw colored, or suffused with red. Blackbrush, other warm desert shrub, shadscale, horsebrush, rabbitbrush, sagebrush, and pinyon-juniper communities at 760 to 2900 m in Beaver, Box Elder, Daggett, Davis, Duchesne, Garfield, Grand, Juab, Kane, Millard, Piute, San Juan, Sevier, Uintah, Utah, and Washington counties; Washington to Montana, south to California, Arizona, and New Mexico; 91 (xvii). This is a valuable browse plant for livestock, especially for sheep. Locally it is called "applebush" because of its palatability. For consideration of relationship to *G. brandegei* see discussion under *Zuckia*.

HALOGETON C. A. Mey.

Annual herbs; leaves alternate, fleshy and sausagelike, bearing an apical slender spine; flowers perfect or partially pistillate, usually bracteolate; perianth of 5 segments, free nearly to the base, embedded in white hair, the segments gibbous, winged in fruit; stamens 2–5, connate basally into a glandular, hypogynous disk; stigmas 2; seeds vertical, laterally flattened, adherent to the pericarp.

Halogeton glomeratus **(Bieb.) C. A. Mey.** Halogeton. [*Anabasis glomerata* Bieb.]. Plants mainly 3–45 cm tall and as broad, glaucous, usually branched from the base, with curved-ascending branches; leaves mainly 3–15 mm long and 1–2 mm thick, terete, dilated and semiamplexicaul basally, obtuse and terminating in a deciduous slender spine ca 1–1.5 mm long, bearing a tuft of hairs and fasicled leaves in the axils; bracteoles ovate; perianth segments membranous, ovate to oblong, 1-veined, with lustrous, membranous, fanlike, veiny wings 2–3 mm long and 3–4 mm wide; stamens united into 2 clusters of 2 or 3, with 1 anther per cluster; fruit oval to obovate, 1.2–1.8 mm long, with an erect cusp on one or both sides. Mainly in disturbed sites in cheatgrass, Russian thistle, salt grass, mixed desert shrub, salt desert shrub, and pinyon-juniper communities at 1220 to 1985 m in most, if not all, Utah counties; widely distributed in western U.S.; adventive from Eurasia; 47 (x). This plant was introduced into northern Nevada in the early 1930s (first collected in 1934), possibly for use in grazing experiments. It spread quickly into the desert lands of Nevada and western Utah, and subsequently into eastern Utah and other states. The plant is rich in oxalates and poses a serious threat to grazing animals, especially to sheep, which have suffered heavy death losses for several decades.

KOCHIA Roth

Annual herbs or subshrubs; leaves alternate (or some opposite), linear to narrowly lanceolate, in some fleshy and terete; flowers 1 to several, sessile in axils of foliose bracts, mostly perfect, 5-merous, the perianth lobes enclosing the fruit, keeled and horizontally winged; stamens mostly 5; stigmas 2 or 3; pericarp thin, free from the horizontal, smooth seed.

1. Plants subshrubs, introduced for reclamation .... *K. prostrata*
— Plants annual or perennial herbs, woody, if at all, only at the base 2
2(1). Plants annual, introduced weeds of disturbed habitats .... *K. scoparia*
— Plants perennial, woody at the base, indigenous in saline habitats .... *K. americana*

Kochia americana **Wats.** Gray Molly. [*K. americana* var. *vestita* Wats., type from shores of the Great Salt Lake; *K. vestita* (Wats.)) Rydb.]. Plants mainly 5–30 cm tall, with erect branches from a woody base; herbage villous-pilose to glabrous; leaves 5–25 mm long, 1–2 mm wide, linear, semiterete and fleshy; flowers solitary or 2–5, sessile in axils of scarcely reduced leaves; inflorescence often more than half the branch length; perianth segments pubescent, at least apically, 1–1.5 mm long, hooded above, somewhat enlarged in fruit, ultimately keeled and with a membranous, striate wing to 2 mm long and 3 mm wide. Greasewood, seepweed, saltbush, saltgrass, matchweed, horsebrush, and pinyon-juniper communities at 1125 to 1985 m in Beaver, Cache, Emery, Garfield, Grand, Iron, Juab, Millard, Salt Lake, San Juan, Sevier, Tooele, Uintah, Utah, and Wayne counties; Oregon to Montana, south to California, Arizona, and New Mexico; 65 (v).

Kochia prostrata **(L.) Schrad.** [*Salsola prostrata* L.]. Subshrubs, mainly 10–75 cm tall; stems erect or steeply ascending, more or less pubescent with short crinkly hairs often intermixed with longer villous ones; leaves 3–12 mm long, 0.3–0.7 mm wide, linear to filiform, flat; inflorescence spiciform to paniculate; flower clusters interrupted; perianth hairy dorsally, the appendages round, flat, and tuberculate or oblong and winglike (ca 1 mm long and 1.5 mm wide), often suffused with red; seeds oval or orbicular in outline, ca 2 mm wide, brown, smooth. This plant is being tried in reclamation plantings and is to be expected throughout Utah; introduced from Eurasia; 1 (0).

Kochia scoparia **(L.) Schrad.** Summer-cypress. [*Chenopodium scoparium* L.]. Annual herbs, mainly 3–12 (15) dm tall, green, or suffused with red in autumn, simple or branching from the base, villous and often finely lanate to glabrous; leaves 0.8–4.5 (6) cm long, 1–4 mm wide, lanceolate to oblanceolate, elliptic or linear, usually 3- to 5-veined, glabrous or softly pilose below (and above) or glabrous above, generally ciliate, acute; inflorescence spicate, interrupted; fruiting perianth of perfect flowers glabrous dorsally, ciliate, mostly transversely keeled, tubercled or sometimes horizontally winged from middle of the keel; pistillate flowers often lacking a keel; seeds ovate in outline, 1.5–2 mm long. Disturbed roadsides, canal banks, field margins, and other waste places in salt marsh, sedge-rush, sagebrush, mountain brush, and pinyon-juniper communities at 850 to 1985 m in probably all Utah counties; widespread in North America; adventive from Eurasia; 38 (ii). The cultivated ornamental phase, with bright red or red-orange foliage is **forma *trichophylla*** **(Hort.) Staph ex Schinz & Thell.** [*K. trichophylla* Hort. ex Voss]. Some workers have suggested that our material belongs to the Russian species *K. iranica* (Hausskn. & Bornm.) Litv. [*Salsola iranica* Hausskn. & Bornm.], but materials examined fit neither key diagnostic nor other discriptive features of that taxon (see Flora SSSR 6:128–134. 1936.

MONOLEPIS Schrad

Annual, polygamo-monoecious herbs; leaves simple, hastately lobed or entire, alternate, mealy to subglabrous, fleshy; flowers unisexual, inconspicuous, borne in axillary clusters; perianth consisting of 1 bractlike scale (rarely 2 or 3, or lacking), not enclosing the fruit; stigmas 2; pericarp reticulately patterned or warty, adherent to the erect seed.

1. Plants dichotomously branched, the ultimate branches filiform; leaves small and inconspicuous, entire; flowers 5 or fewer per axillary cluster; perianth segments 1–3, linear; plants rare .... *M. pusilla*
— Plants not dichotomously branched, the ultimate branches not filiform; leaves conspicuous, commonly at least some hastately lobed; plants common .... *M. nuttalliana*

Monolepis nuttalliana (Schultes) **Greene** Poverty-weed. [*Blitum nuttallianum* Schultes in R. & S., based on *B. chenopodioides* Nutt.; *M. chenopodioides* (Nutt.) Moq. in DC.]. Plants mainly 4–30 cm tall, the stems prostrate or ascending to erect, simple or much branched from the base, mealy to subglabrous; leaves 5–50 mm long, the blades 1–15 mm wide, lanceolate to elliptic or oblong, with one pair of lateral lobes near the middle, reduced upward and sometimes entire, the petiole 1–20 mm long; flowers borne in dense, sessile, axillary clusters; perianth segments 1–2 mm long, more or less acute apically; pericarp pitted, usually pale; fruit 0.9–1.5 mm broad. Pioneer plant of open sites in blackbrush, shadscale, mat saltbush, sagebrush, pinyon-juniper, mountain brush, ponderosa pine, Douglas fir-limber pine, aspen, and lodgepole pine communities at 350 to 3355 m in probably all Utah counties; Alaska and Yukon to California and New Mexico, east to Manitoba and Missouri; 70 (xiv). The correct name for this plant seems to be *M. chenopodioides*, there being no apparent obstacle to the transfer of *Blitum chenopodioides* to *Monolepis*. However, I hesitate to suggest the change until further research corroborates such a necessity.

Monolepis pusilla **Torr. ex Wats.** Plants clump-forming, 3–20 cm tall and as broad or wider; leaves 4–12 mm long, oblong, entire, short-petioled; flowers 1–5, in sessile clusters; sepals spatulate, obtuse, 1–3; pericarp tuberculate; seeds dull, ca 0.5 mm wide. Salt desert shrub at ca 1500 m in Uintah County (Holmgren et al. 1934 BRY); Oregon to Wyoming, south to California and Nevada; 1 (0)

NITROPHILA Wats.

Perennial rhizomatous herbs from a definite caudex; leaves opposite, linear to oblong, fleshy, clasping, entire; flowers perfect, axillary, 2-bracteolate, solitary or in 3s; calyx chartaceous, with 5 sepals, these keeled, 1-veined; stamens 5, united basally into a perigynous disk; style filiform, with paired stigmas; fruit ovoid, beaked, included in connivent sepals; seeds vertical, lenticular.

Nitrophila occidentalis (Moq.) **Wats.** Niterwort. [*Banalia occidentalis* Moq. in DC.]. Plants glabrous, mainly 10–30 cm tall; stems with opposite branches, erect or ascending; leaves 0.7–2 cm long, linear, semi cylindirc, sessile, mucronate; flowers sessile; sepals 2–3 mm long, oblong, stramineus (pinkish when fresh); fruit brown; seed shining, black, ca 1 mm wide. Saline clay substrate in saltbush, pickleweed, alkali saccaton community in Snake Valley, Millard County (Welsh, Taylor, and Thorne 14516 BRY); Oregon to California, Nevada, and Mexico; 1 (i).

SALICORNIA L.

Annual or perennial herbs from taproots or rhizomes; leaves simple, scalelike, opposite, connate, glabrous; flowers perfect, borne sessile in opposite groups of 3, sunken in depressions of thickened, terminal spikes, subtended by scalelike bracts; perianth consisting of 4 connate segments free at the tip around a slitlike opening, enclosing the fruit; stigmas commonly 2; pericarp thin, free from the erect, retrorsely pubescent seed.

1. Plants annual, from slender taproots, the main stems mostly less than 3 mm thick; central flower much above the lateral ones .... *S. europaea*
— Plants perennial from thick rhizomes and fibrous routs, the main stem mostly more than 3 mm thick; central flower not much above the lateral ones .... *S. utahensis*

Salicornia europaea **L.** Annual Samphire. [*S. rubra* A. Nels.; *S. europaea* ssp. *rubra* (A. Nels.) Breitung; *S. trona* Lunnel; *S. europaea* var. *trona* (Lunnel) B. Boi.]. Annual Samphire. Plants annual, mainly 9–30 cm tall, from slender taproots; stems fleshy, erect or ascending, commonly branched, often reddish at maturity; leaves scalelike, often with a scarious margin; spikes 0.5–5 cm long, 2–3 mm thick, the joints 2–4 mm long; central flower much above the lateral ones; fruit dehiscent, the seeds falling separately. Saline substrates in salt marsh, seepweed, poverty weed, alkali saccaton, and saltgrass communities at 1280 to 1465 m in Box Elder, Cache (?), Juab, Millard, Salt Lake, Tooele, Uintah, and Utah counties; widespread in North America; Eurasia; 19 (ii). Our specimens are supposed to differ from the more coastal ones in having slender spikes with joints about as thick as long, but no such correlation is apparent. Recognition of our material at infraspecific level seems moot.

Salicornia utahensis Tidestr. Utah Samphire. [S. *pacifica* Standl. var. *utahensis* (Tidestr.) Munz]. Plants perennial, mainly 9–30 cm tall, from coarse rhizomes and thick fibrous roots; stems fleshy, erect or ascending, not creeping and rooting at the nodes, turning gray or brown at maturity; leaves scalelike, with scarious margins; spikes 0.6–5 cm long, 3–4 mm thick the joints 3–5 mm long, breaking at the joints when mature, the central flower not especially above the others; fruit dehiscent, the seeds falling separately, sometimes adherent to the calyx. Saline substrates in salt marsh, pickleweed, and saltgrass communities at 1280 to 1405 m in Box Elder, Millard, Salt Lake, Tooele (type from shore of Great Salt Lake), and Utah counties; endemic ? (reported from California?); 11 (ii). Our material differs markedly from the similar coastal species assigned to either S. *pacifica* Standl. or S. *virginica* L.

SALSOLA L.

Annual herbs; leaves alternate, entire, commonly spinulose; flowers perfect, 5-merous, solitary or clustered in axils of spiny bracts, each with 2 smaller bracteoles, borne in spicate inflorescences; fruiting perianth with winglike, mostly horizontally spreading ridges; stamens 5, usually inserted at the margin of a lobed disk; styles 2 or 3; fruit closely enveloped in the persistent calyx; seeds horizontal to oblique.

BEATLEY, J. C., 1973. Russian thistle (*Salsola*) species in western United States. J. Range Management 26:225–226.

1. Leaves mainly 0.3–1.8 mm wide and 1.5–4 (6) cm long, slender; wings of fruiting calyx usually 1–2 mm long .... S. *iberica*

— Leaves mainly 1–1.5 mm thick and 0.5–2 cm long, thick and rigid; wings of fruiting calyx mainly 3–4 mm long .... S. *paulsenii*

Salsola iberica **Sennen & Pau** Russian-thistle; tumbleweed. [S. *pestifer* A. Nels.; S. *kali* authors, not L.?]. Plants with simple stems or freely branched, clump-forming, appearing taller than wide, 1–10 dm tall; stems with red-purple, longitudinal striations, glabrous or pubescent; leaves mainly 1.5–4 (6) cm long, 0.3–0.8 mm wide, narrowly linear or filiform, spinulose apically, modified upward as spinescent bracts with expanded bases and scarious margins; perianth segments distinct, membranous in anthesis, in fruit becoming transversely winged, the wings mainly 1–2 mm long; seeds horizontal. Weedy species of disturbed habitats at 760 to 2440 m in probably all Utah counties; widespread in North America; adventive from Asia; 62 (vi). This species forms intermediates with the next. It is unfortunate that so many specific epithets have been applied to this weedy introduction, and possibly even the above name is not unequivocally correct.

Salsola paulsenii **Litv.** Barbwire Russian-thistle. Plants commonly freely branched, clump forming, appearing wider than tall, mainly 10–40 cm tall and usually broader; stems yellowish green, seldom purplish striate, pubescent or glabrous; leaves mainly 0.5–2 cm long, 1–2 mm thick, linear, rigid, spinose apically, modified upward as spinose bracts with wide bases and scarious margins; perianth segments yellowish, membranous in anthesis, becoming transversely winged, the wings 2–4 mm long in fruit; seeds horizontal. Weedy species of disturbed habitats at 915 to 1830 m in Carbon, Garfield, Juab, Kane, Millard, Tooele, Washington, and Wayne counties; Arizona, Nevada, and California; 12 (iii). A third species, S. *collina* Pallas, might be present in Utah. It has long slender spicate inflorescences with appressed bracts and bracteoles, and in the lower portions the flowers are usually gall-like.

Sarcobatus Nees

Thorny shrubs; leaves mostly alternate, linear, fleshy, sessile; flowers imperfect, borne in axillary spikes, the staminate ones spirally arranged, ebracteate, and lacking a perianth; stamens 2 or 3, borne beneath stalked peltate scales; pistillate flowers sessile, 1 or 2, in the axils of scarcely reduced leaflike bracts, the pistil surrounded by a cuplike, shallowly lobed to subentire perianth, this accrescent and adherent to the fruit base, its upper portion flaring to form a broad, winglike border; seeds erect, flattened, orbicular.

***Sarcobatus vermiculatus* (Hook.) Torr. in Emory.** Greasewood. [*Batis (?) vermiculata* Hook.; *Fremontia vermicularis* (Hook.) Torr. & Frem.]. Shrubs, mainly 10–20 dm tall or more; branches rigid, spreading, often modified as thorns; leaves 0.3–4.5 cm long, 1–3 mm wide, semicylindric, linear; staminate spikes catkinlike, 1–4 cm long; pistillate flowers fewer than the staminate ones, the perianth ca 1 mm long; calyx wing 2–6 mm long; fruit 4–5 mm long, cup shaped below the wing; seeds brown, ca 2 mm long. Greasewood, seepweed, saltbush, and other plant communities of saline substrates, at 1220 to 2170 m in most if not all Utah counties; Washington and Alberta to North Dakota, south to California, Arizona, New Mexico, and Texas; 72 (x). This is an important browse species for cattle and sheep, even though potentially poisonous.

Spinacia L.

Annual or biennial glabrous herbs; flowers borne in dense spicate inflorescences; pistillate flowers lacking a perianth, but with 2 (rarely 3 or 4) persistent bracteoles that enlarge, become connate, and harden in fruit; stigmas 4 or 5; seeds vertical.

***Spinacia oleracea* L.** Spinach. Plants mainly 2–6 dm tall or more, erect; leaves mainly 3–15 cm long and 2–10 cm wide, ovate to triangular, often hastately lobed; bracteoles in fruit orbicular to obovate, often with a spreading spine at the apex. Cultivated potherb throughout Utah, mainly below 2135 m; introduced from Eurasia; 1 (0). This plant escapes occasionally, but does not persist.

Suaeda Forsk. ex Scop. Nom. Cons.

Annual or perennial herbs or shrubs; leaves alternate, entire, terete or flattened, often succulent; flowers inconspicuous, mostly perfect, solitary or clustered in leaf axils, bracteate; calyx 5-lobed, fleshy, the lobes equal and unappendaged or unequal and some more or less corniculately appendaged; stamens 5, the filaments short; ovary subglobose or depressed; seeds horizontal or vertical.

1. Plants suffrutescent or definitely shrubby; leaves abruptly short-petiolate; calyx lobes equal, not appendaged, smooth dorsally; herbage glabrous or puberulent; seeds vertical or horizontal .... *S. torreyana*

— Plants annual; leaves sessile; calyx lobes unequal in fruit, horned; herbage glabrous; seeds horizontal 2

2(1). Plants often over 3 dm tall, erect, not clump-forming, the branches stiffly erect-ascending; flowers mostly 3–7 per axil .... *S. calceoliformis*

— Plants mainly 0.5–3 dm tall, forming depressed rounded clumps, the branches spreading, more or less flexuous; flowers 1–3 per axil .... *S. occidentalis*

***Suaeda calceoliformis* (Hook.) Moq.** Broom Seepweed. [*Chenopodium calceoliforme* Hook.; *S. depressa* authors, not (Pursh) Wats.; *S. depressa* var. *erecta* Wats.]. Plants glabrous, often glaucous, erect, simple or with erect-ascending branches and broomlike, 1–5 (8) dm tall; leaves mainly 1–4 cm long, 1–2 mm wide, linear or tapering from base to apex, semiterete, intergrading with floral bracts upward; spikes slender; flowers sessile, mostly in clusters of 3–7; calyx lobes unequal, ca 1.5 mm long, at least some conspicuously horned; fruit horizontal; seeds smooth, 1–1.5 mm wide, dark brown. Saline palustrine or riparian sites in saltgrass, greasewood, seepweed, alkali saccaton, and cattail-sedge communities at 850 to 2440 m in Box Elder, Cache, Davis, Duchesne, Emery, Grand, Millard, Salt Lake, Sanpete, Sevier, Uintah, Utah, Washington, and Weber counties; British Columbia to Saskatchewan, south to California, Arizona, New Mexico, and Texas; 35 (vi).

Suaeda occidentalis **(Wats.) Wats.** Western Seepweed. [*Schoberia occidentalis* Wats.]. Plants glabrous, often glaucous, forming depressed rounded clumps, not broomlike, mainly 0.5–3 dm tall, seldom simple; leaves mostly 0.5–2 (3) cm long, linear-oblong, semicylindric, intergrading with floral bracts upward; spikes slender; flowers sessile, mostly 1–3 per cluster; calyx lobes unequal, ca 1.5 mm long, at least some conspicuously horned; fruit horizontal; seeds smooth 1–1.5 mm wide, dark brown. Saline palustrine or riparian habitats in greasewood, saltgrass, seepweed, and other such communities at 1280 to 2135 m in Beaver, Box Elder, Cache, Duchesne, Salt Lake, Sevier, and Utah counties; Washington to Wyoming, south to Nevada and Colorado; 12 (i).

Suaeda torreyana **Wats.** Torrey Seepweed. Plants glabrous or pubescent, sometimes glaucous, suffrutescent or definitely shrubby, 1–12 (15) dm tall or more, with slender ascending to spreading branches; leaves 0.5–3.5 cm long, 1–3 mm thick, subterete to flattened, abruptly short petiolate, intergrading with floral bracts upward; flowers 1–8 or more per axil; calyx lobes equal, ca 1.5–2 mm long, the lobes merely rounded dorsally, not horned or tuberculate; fruit horizontal or vertical; seeds 0.8–1.2 mm wide, black, shiny. Greasewood, seepweed, saltgrass, and other salt desert shrub communities, often in riparian or palustrine habitats at 1125 to 1955 m in Box Elder, Duchesne, Emery, Garfield, Grand, Juab, Kane, Millard, Salt Lake, San Juan, Sevier, Tooele, Uintah, Utah, and Wayne counties; California, Nevada, Wyoming, Arizona, and Mexico; 79 (xiv). Materials cited with the above description belong to var. ***torreyana*** [*Chenopodina linearis* Torr., type from Great Salt Lake; *C. nigra* authors, not (Raf.) Macbr.] A second variety, sometimes treated at specific rank, is based on densely puberulent plants. It is var. ***ramosissima*** **(Standl.) Munz** [*Dondia ramosissima* Standl.; *S. intermedia* Wats., type from Sevier or Washington counties]. Saltgrass, shadscale, greasewood and other salt desert shrub communities at 850 to 1400 m in Juab, Millard, Salt Lake, Sevier, and Washington counties; Arizona and California; 11 (0). Phases of this variety from Washington County seem to have more steeply ascending and more elongate branches than those from elsewhere in Utah. Possibly all of the variants are taxonomically neglegible.

ZUCKIA Standl.

Dioecious or less commonly monoecious shrubs or subshrubs; branches not thorny; axillary buds subglobose, porminent; leaves alternate, entire or more or less lobed; herbage more or less scurfy; staminate flowers 2–5 in clusters in bract axils, not separately bracteolate, the perianth 4- or 5-lobed, subequal to the 4 or 5 stamens; pistillate flowers 1 to several per bract, often some vestigial, each enclosed by 2 bracteoles, these dorsiventrally flattened and unequally 6-keeled or obcompressed and thin-margined, often subtended by a single filiform bractlet; fruits vertical or horizontal; stigmas 2.

Zuckia brandegei **(Gray) Welsh & Stutz** comb. nov. Siltbush. [based on: *Grayia brandegei* Gray Proc. Amer. Acad. 11:101. 1976]. Plants mainly 1–5 dm tall; branching from a persistent woody base ca 0.5–2 dm tall, the annual stems erect or ascending; herbage more or less scurfy and less commonly with some moniliform hairs in inflorescence; leaves subsessile or tapering to a short petiole, 13–80 mm long, 15–42 mm wide, linear or narrowly oblanceolate-spatulate to elliptic, ovate, obovate, or orbicular, entire or rarely hastately lobed; staminate flowers with a 4- or 5-lobed stramineous perianth, cleft to the middle or below, ca 1.5–1.8 mm long; pistillate bracts obcompressed or dorsiventrally compressed, with vertical or horizontal fruits, respectively, but not exclusively, when mature either flattened and 4–8 mm wide or 6-keeled (with 4 small and 2 large keels) and 2–4 (5) mm wide; fruits included within the bracts. It has long been recognized that *Grayia brandegei* was not a close congener of *G. spinosa*, type species of the genus *Grayia*, even though they shared features of bract compression and rounded axillary buds. They differ markedly in gross morphology, in vesture, and in nature of the bracts. The bracts of *G. spinosa* are thickened marginally, and filled internally with a spongy cellular matrix. Those of *brandegei* are thin margined, and do not possess a spongy cellular matrix. Some workers have suggested that *G. brandegei* should be removed from its long association with *G. spinosa* and placed within the *gardneri* phase of *Atriplex*. The differences between *Z. brandegei* and any of the *Atriplex* species are striking even though the plants in vegetative condition might be confused. Bract and bud differences in *Zuckia* are correlated, apparently, with C–3 type of photosynthesis and its attendant foliar morphology, and the shrubby atriplexes have the C–4 type of photosynthesis with its foliar morphology. Two more or less distinctive but intergrading phases are present.

1. Fruit dorsiventrally compressed; bracts 6-keeled; fruit mostly horizontal .... *Z. brandegei* var. *arizonica*
— Fruit obcompressed; bracts 2-winged, samaralike; fruit mostly vertical .... *Z. brandegei* var. *brandegei*

Var. *arizonica* (Standl.) Welsh comb. nov. [based on: *Zuckia arizonica* Standl. J. Washington Acad. Sci. 5:58. 1915]. Fine-textured or sandy, often saline and seliniferous substrates on Entrada, Morrison, and Duchesne river formations in Emery, Uintah, and Wayne counties; Arizona; 10 (i). Despite the distinctive bracts and horizontal fruits, the plants are well within the range of vegetative variation existing in plants of *Z. brandegei* in a strict sense. Staminate plants of this variety have not previously been discerned from among the general collections of *Z. brandegei*. Previous descriptions of *Zuckia* and its only species (*arizonica*) are conspicuous in lacking discussion of staminate features. Supposed differences in vesture between the taxa apparently do not exist, and other diagnostic morphology is unknown.

Var. *brandegei* Fine-textured, often saline and seleniferous substrates on the Duchesne R., Uinta, Kaiparowits, Summerville, Morrison, Chinle, and Moenkopi formations (and probably others) at 1280 to 2440 m in Daggett, Emery, Garfield, Grand, Kane, San Juan, Sevier, Uintah, and Wayne counties; Colorado and Arizona; 66 (xii). Both broad and narrow-leaved phases of both varieties are known, and there is a tendency for the wideness of leaves to be geographically correlated (i.e., the broad-leaved populations from the Uinta Basin and those on "The Blues" of the Kaiparowits Formation northeast of Henrieville and north of Four-Mile Bench), but the plants differ in no other discernible way. Probably these variants do not warrant taxonomic recognition.

IN MEMORIAM: SEVILLE FLOWERS (1900–1968)

William H. Behle[1]

ABSTRACT.— Seville Flowers was the foremost authority of his time on cryptogamic botany in the intermountain region, having published monographs on the mosses, lichens, and ferns of Utah. He also had strong interests in algae, grasses, composites, and the history of botany. In addition to his systematic research, his expertise extended to field ecology. Early in his career he made a classic study of the vegetation of the Great Salt Lake region that led in later years to his participation in the ecological studies at Dugway Proving Grounds in western Utah. Still later he had charge of the predam vegetative surveys of several reservoir sites along the Upper Colorado River, including Glen Canyon, which was later submerged under Lake Powell. He served as professor of botany at the University of Utah from 1936 to 1968. His professional career started in 1929. A bibliography of his writings is included in this account of his life and professional career.

Many people naturally remarked that Dr. Flowers's surname was very appropriate for a botanist, and one might suppose that after years of exposure to trite expressions concerning this he would have become annoyed. Instead he displayed a good-natured, even delightful, sense of humor. This is illustrated by a remark he made when introduced to a graduate student in the biology department whose name was Miriam Bloom. He quickly said to her, "My dear, you and I ought to write a botany text together." Although he was an authority on the higher plants, his specialty areas pertained more to the lower orders of nonflowering or cryptogamic plants, namely the liverworts, algae, lichens, mosses, and ferns. As regards the flowering plants, he had strong interests in the grasses as well as the Compositae. Overall he was a well-trained and versatile student of the whole plant kingdom, particularly the flora of western North America and Utah.

His research covered a wide spectrum of interests. At one extreme, based on extensive field studies, were broad-scale regional plant inventories and ecological floral analyses. At the other end were microscopical anatomical studies on lower plants or structural details of the anatomy of higher plants. He was remarkably proficient as an artist, a gift that enabled him to illustrate his original descriptions of plants, his monographs on the mosses, hepatics, and ferns of Utah, as well as numerous teaching and laboratory manuals.

Other less-well known attributes were his skills as a landscape painter, musician (piano), and student of Latin and Greek. His interest in ancient languages was doubtless correlated with the practice in botanical circles of formally describing new species and varieties in Latin, as well as the utilization of Latin and Greek words for scientific names. His paintings depicted striking scenes in Utah where his field work took him. In the quiet of his home during rare unoccupied evenings, he enjoyed reading classical literature. In the field, around a campfire, he was an accomplished raconteur, a feature he shared with his close friend and colleague Stephen D. Durrant. I suspect that many of Steve's stories and jokes came from Bill Flowers. Bill would tell them with a dry humor, and Steve would enliven them with his own embellishments in the retellings. Bill enjoyed a good cigar occasionally and often smoked a pipe. In a less tolerant era at the University of Utah, to do so he had to frequent restricted smoking areas in secluded, designated spots behind certain buildings, one of which was behind the administration (Park) building near the former greenhouse. Here he picked up many stories and jokes from kindred spirits.

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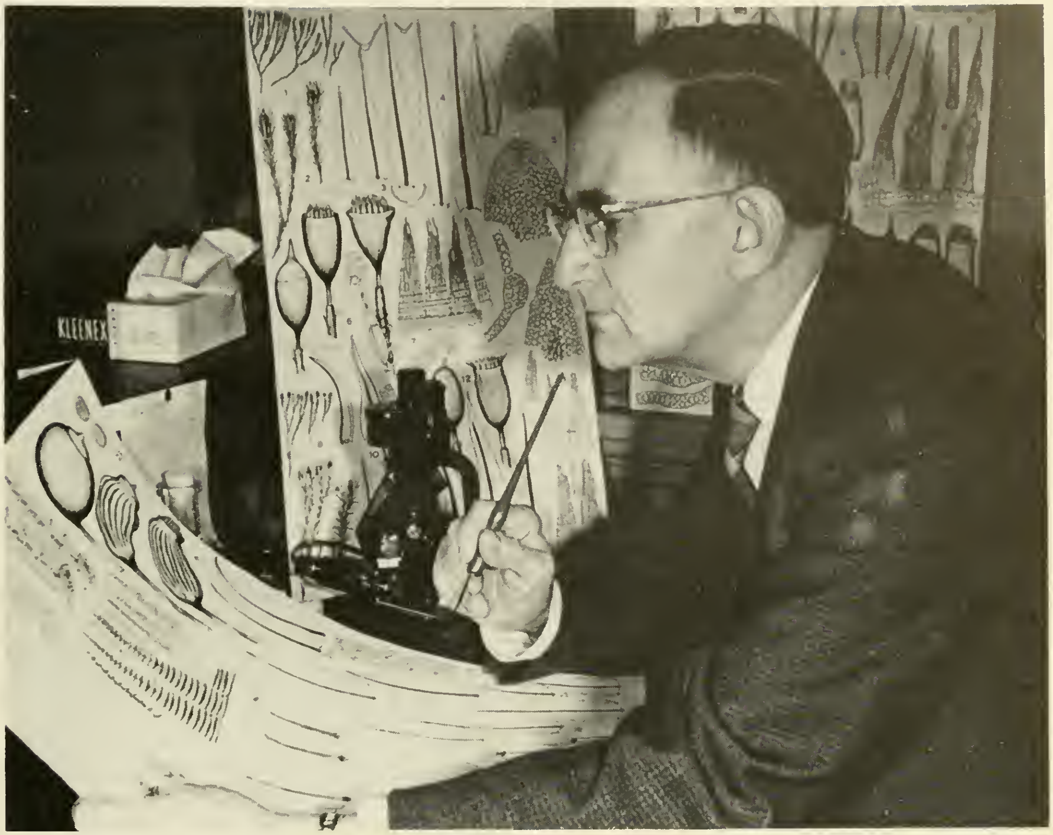

Fig. 1. Seville Flowers (ca 1967) in his laboratory preparing illustrations for his monograph on the mosses of Utah and the West.

He was regarded as being somewhat absentminded, and indeed he was often preoccupied with his research. He became "hard of hearing" in his later years. Both of these traits I think he deliberately used to miss committee or staff meetings or other events in which he had little or no interest. His thoroughness in teaching and attention to detail appealed especially to botany majors and graduate students. In his research he made a great impact on the field of botany both in Utah and nationally. The following memorial on his life and work portrays his distinctive personality and highlights his many contributions in his professional field.

Seville Flowers was born in Salt Lake City, Utah, on 14 January 1900, the son of John and Caroline Flowers. He had one brother and two sisters. He was christened Bradnum Saville Flowers, but he didn't care for the first and middle names, so early in life he elected to be known simply as Seville Flowers. His mother fondly called him Billy which evolved to Bill in later life. Curiously, for a short time he even signed his name W. S. Flowers as though Bill was a nickname for William.

In his childhood he lived for a time in Long Beach, California, when his mother was advised by her doctor to live at sea level for her health. They stayed in the Signal Hill area. Bill often told the story, probably recalling from secondhand sources rather than memory, that his mother was constantly admonishing him not to play in the creek near their home because he got so covered with oil from the water!

All his early education was obtained in Utah, commencing in grade school in 1907. The family home was in the avenues section on the north slope of the city, which at the time was a sparsely populated area. Consequently, as a youth he and his companions roamed freely through the foothills, along the bench, and in the mouths of several shallow nearby canyons, thus gaining an intimate acquaintance with nature and a firsthand knowledge of the common local plants and animals. He once remarked to the writer that the urge to know more about the flora and fauna became an obsession with him. His interest in nature may have been partially innate, but it was certainly also conditioned by these early sorties, rather than being inspired initially by some great teacher. Influence from this source came later.

In addition to having an inquiring mind, he liked to draw things. Consequently, while attending East High School and facing the necessity of selecting an area of specialization, he was attracted to mechanical drawing. He even envisioned a career as an architect or civil engineer. Although the study of plants and animals constituted a powerful attraction, he shied away from biology courses, rationalizing that the study of botany and zoology represented an occupation that was reserved either for those who were financially independent or for just a scholarly few. He certainly wasn't financially well off and didn't consider himself to be intellectually gifted. The idea of his ever becoming a teacher or researcher simply never occurred to him. The writer's aunt, Jessie Harroun, had Bill Flowers as a student in one of her classes in English at East High School. She remembered him as being a quiet but excellent student and said that he participated in track as a distance runner.

Upon graduation from high school he started attending the University of Utah in the autumn of 1920 and, in keeping with his earlier intention, enrolled in the School of Engineering, where he spent two years. On the side, as part of a liberal education, this time he did take courses in botany and zoology, but there were few courses then being offered in the latter field. In some brief biographical notes prepared not long before his death, he wrote that one day the dean of the Engineering School called him in to his office and pointed out that his grades in engineering courses were mediocre, whereas those in biological subjects were much higher, which suggested that he was in the wrong field. Besides, the dean remarked "there was not enough money in the country to build the elaborate structures appearing on my drawing boards and that I would be an unhappy architect faced with the reality of having to design simple, practical structures 'like steel bridges, not Greek temples.' With reluctance I allowed architecture to fade from my program."

Having been thus discouraged from either architecture or engineering, he decided to pursue his true love of biology, more particularly botany. He faced a dilemma, however, because botany was at a low ebb at the university, and there were not enough courses to constitute a major. Seville adjusted to this in a most unusual way. A. O. Garrett, who taught botany at East High School and was supervisor of the science program there, was one of the few trained botanists in the state. Incidentally, the herbarium at the University of Utah was later named in his honor as the Garrett Herbarium. So after two years at the university, Bill Flowers returned to high school, where he took every course offered by "Professor" Garrett.

Another influence in his life was the alpine school at Aspen Grove back (east) of Mt. Timpanogos conducted each summer by Brigham Young University in the 1920s. One summer Dr. Henry C. Cowles, an internationally known pioneer plant ecologist at the University of Chicago, was guest professor. He attracted some out-of-state students from various parts of the country as well as many local students, one of whom was Seville Flowers. If there was any lingering doubt in Bill Flowers's mind about what he wanted to do for his life's work, the association with Dr. Cowles and the outside students clinched the choice. For the following two summers Dr. Cowles taught at the Utah State Agricultural College at Logan, and Bill Flowers followed him there to take whatever courses were offered. By dividing his time between East High School, the University of Utah, Brigham Young University, and Utah State Agricultural College, he was able to fulfill a major in botany that was acceptable to the University of Utah, and the A.B. degree was granted by that institution in June 1925.

During the summer of 1925, Mr. Garrett was a guest instructor at the BYU summer school, and one of the classes he offered was on mosses. Bill Flowers attended BYU's summer school once again to take this class. There were six students enrolled. About that time A. T. Beals, who was secretary of the Sullivant Moss Society, wrote to Mr. Garrett making an offer to have specimens of Utah mosses identified by leading authorities, provided that duplicates were sent for each specialist to keep for his personal collection. Mr. Garrett accepted the proposition and during that summer had the members of his class collect mosses from Mt. Timpanogos and vicinity. About 500 samples were sent to Beals. (Incidentally, one of the specialists who participated in the identifications was Edwin B. Bartram. Afterwards, Bill Flowers kept up a correspondence with him for many years and exchanged specimens. When Flowers himself became an authority, Bartram would periodically send him specimens to identify.) When the results of the summer collecting were returned to Mr. Garrett, 85 species of mosses had been identified. These were turned over to Bill Flowers for study, and he presented the results as a dissertation entitled *The Moss Flora of Mount Timpanogos* to Brigham Young University for the master's degree. The M.A. degree was awarded him in 1926. His first publication (1929) was a preliminary list of Utah mosses based largely on the Mt. Timpanogos study. Ultimately, 471 specimens were presented to Bill Flowers by Mr. Garrett. These became the nucleus of his personal collection, which grew throughout the years until at the time of his death there were in excess of 5,000 specimens.

Faced now with the necessity of earning a livelihood, he commenced a teaching career at Carbon County High School in Price, Utah, in the autumn of 1926. He taught botany and zoology there continuously up to 1930. By this time he was imbued with the desire to obtain the Ph.D. degree, which was unusual for a high school teacher in those times. Here again the influence of Dr. Cowles was manifest, for Flowers went to the University of Chicago to study under him. He was appointed a Fellow and spent the academic years of 1930–31 and 1931–32 there. As previously noted, Dr. Cowles was an ecologist, hence a morphological or systematic problem on mosses was not suitable for a dissertation. So Flowers elected to work on the vegetation of the Great Salt Lake region. Dr. Cowles's sorties to Utah had made him aware of the potential for such a study in the unique environment of western Utah. For this particular research Bill Flowers needed a background in soil chemistry, but he was prepared for this since he had taken numerous courses in chemistry along the way. His research on this topic was characteristically thorough. The report (Flowers 1934a, see also 1942b) constitutes one of his major publications and established his reputation as an ecologist as well as a morphologist and systematist. The Ph.D. degree was conferred on him in 1932. Following this achievement, he returned to Utah to resume teaching at Carbon County High School, which he continued to do through the 1935–36 academic year. Incidentally, my first contact with Bill Flowers came at the University of Utah during the late summer of 1932 in the interval between his leaving Chicago and reporting at Price. As a graduate student in zoology studying the colonial nesting birds of the islands of Great Salt Lake, I sought his help to identify some plants I had obtained on Hat and Gunnison islands. I found him in a corner of one of the laboratories in the biology building surrounded by mosses that he had collected in the Great Salt Lake region. We had much to talk about, and he was most cordial and helpful. He was preparing a separate paper (1933c) on the mosses of the Great Salt Lake region. He joined the teaching staff at the University of Utah one year prior to my affiliation (1936 vs. 1937). We were close friends and colleagues for the next 31 years.

The summer of 1933 he spent in Salt lake City reworking his doctorate dissertation for publication. On 29 November 1933 he married Emily Jones of Salt Lake City. Two children came of this union, John and Frances Flowers.

The following year Dr. Flowers had one of the greatest experiences of his life when two months were spent studying with the preeminent authority of the times on the mosses of North America, A. J. Grout. In his later years, Dr. Grout had developed a routine of spending winters at his home in Manatee, Florida, and summers at his cottage at the small New England village of Newfane, Vermont. His home there was known as Moss

Rock Cabin and was situated high on a hill overlooking the village and surrounding terrain. Near the home there was a small building that served as his laboratory and housed his herbarium and library. It became his custom to have three or four students come each summer and live with him and his wife and study with him. Eventually, he built a little guest cottage. Dr. Flowers was one of the select few chosen to study with him during the summer of 1934.

Enroute from Utah, Bill and Emily spent about two weeks at the University of Chicago and then continued on to New England. Emily stayed in New York for two weeks before rejoining her husband. In the meantime Bill arrived at the Grout home about 2:00 a.m. and, not wanting to awaken anyone, slept in the car. They were assigned quarters in the newly built cottage. Dr. Grout invited them to use vegetables from his garden and apples from his trees. Several years later Dr. Flowers (1947) wrote a brief account of this summer with Dr. Grout. His article was accompanied by two sketches, one of the house, the other of the laboratory building. These were dated 12 and 17 August 1934 and constitute evidence of Dr. Flowers's skill as an illustrator. Dr. flowers received a certificate from the Biological Laboratory at Cold Springs Harbor for his postgraduate work with Dr. Grout.

While teaching at Carbon County High School, Dr. Flowers served as state chairman for the National Education Association Science Department for the years 1934, 1935, and 1936. He was also chosen president of the Biological Science Section of the Utah Education Association for 1935–36 and 1936–37. During the summer quarter of 1935, Dr. Flowers offered a course in bryology at the University of Utah, the first time that such a course had been offered. Arthur Holmgren took the course and was greatly impressed by Dr. Flowers's enthusiasm for the subject.

Starting with the academic year 1936–37, Dr. Flowers became a member of the Department of Biology at the University of Utah. At last he had found his proper niche in the academic world. He continued his teaching and scholarly research at that institution for the next 32 years, becoming one of the foremost authorities in the country on mosses, ferns, and other cryptogams. Through the years he was assigned to teach many sections of the required general biology course and numerous general education botany courses, as well as courses in his specialty areas.

His committee assignments were not numerous because of his preoccupation with research, but he served many years on the Scholastic Standards Committee. He was active in the local chapters of Phi Sigma Biological Society and Sigma Xi and in the Utah Academy of Sciences, Arts, and Letters. His out-of-state professional affiliations were with the American Institute of Biological Sciences, Phycological Society of America, American Fern Society, American Society of Plant Taxonomists, and International Association for Plant Taxonomy.

His closest working relationships were, of course, with the professional and amateur bryologists throughout the country. Many of his publications appeared in the journal the *Bryologist*. This was the organ of the American Bryological Society that had evolved from the Sullivant Moss Society. About 1944 he served as a member of a committee of the Sullivant Moss Society, along with H. S. Conrad (chairman), P. M. Patterson, and F. E. Wynne, which was charged with studying and reporting on techniques pertaining to the proper preparation and care of a moss collection (see Conrad et al. 1945). Many years later Dr. Flowers (1956b) described a new method of cutting sections of moss stems and leaves. He served as vice-president of the American Bryological Society for 1964–65 and became president in 1966–67.

The dedication and altruistic nature of the man is indicated in one early paper (1937c) where he announced the availability of copies of an index that he had prepared for all the species of mosses, hepatics, and lichens that had been described in the *Bryologist*. This listed all the titles of articles, citations to volume, year, and page, the names of species described, and any special references that might be difficult to find. It extended from volume 1 through 40. He cut the stencils himself on his own typewriter. He originally intended to offer copies to members of the society for just the cost of the postage, but the expense was so great that he found it necessary to charge each recipient one dollar. The initial product consisted of about 50 mimeographed pages. He planned to issue new sheets each year to update the venture. How long he persisted in this is not known to the writer. Neither do I know how many of the annual forays of the society that he attended, but I recall his mentioning going on one to Oregon, and he served as reporter for the trip in 1964 to parts of Colorado (Flowers 1965c).

Several features stand out in connection with the research of Dr. Flowers. One was the wide coverage of subjects that he dealt with. Another was his meticulous work and superb illustrations. A third was his slow, deliberate, thorough approach. This was due in part to his correlating research with teaching. He literally spent years working (at times intermittently) on various projects. He would often prepare a preliminary list of some group of plants, add to it as new knowledge accumulated, submit the paper to peers for review, and finally would publish a comprehensive review or monograph. Another technique was to issue mimeographed handouts for students to use in his classes. Mostly, he cut the stencils, ran off the sheets, and assembled the pages personally. Sometimes he even purchased the stencils and paper himself. Only after the work had been subject to critical scrutiny over a long period and after corrections and revisions had been made to his satisfaction did he feel it was ready for formal publication.

Perhaps the best way to illustrate all these features is to discuss his contributions in each of several groups of plants or topics that he worked with, starting with the mosses representing the Class Musci of the Phylum Bryophyta. It was this area of his work that was most extensive and well known. Significantly, the first publication in his bibliography of 74 titles was the preliminary list of Utah mosses (1929), and the last, published posthumously, was his 566-page book *The Mosses of Utah* (1973). In between were several progressive stages of research.

After the preliminary list he published a short article on fossil mosses (1933a) and then, in connection with his research for the doctorate, prepared the list (1933c), *Mosses of the Great Salt Lake Region*. Then came a 48-page mimeographed summary (Flowers 1935a) entitled *The Mosses of Utah*, which he privately published while teaching in Price. Five hundred were assembled and copies placed in the libraries of all the universities and colleges in the state. Next, *The Bryophytes of Utah* (Flowers 1936) appeared in the *Bryologist*. In this publication he not only itemized the species known to occur in Utah, but also correlated their geographical distribution with the vegetative zones and higher plant communities in Utah.

His magnum opus on the mosses of Utah, on which he had worked for over 40 years, had been essentially completed at the time of his sudden death. Fortunately, he had submitted it for review to three friends and eminent bryologists, William C. Steere, Lewis E. Anderson, and Howard A. Crum. Dr. Crum, more than any other person, brought the work into publishable form. He meticulously worked over the entire manuscript, which was nearly 700 typewritten pages in length, and, since he was one of the best students of mosses in North America, the manuscript benefitted greatly from his knowledge and editorial critique. Unfortunately, he was not given credit for his contribution in the book due to an oversight attributed to its publication several years after completion, with little continuity between.

Actually, after Dr. Flowers's sudden death the manuscript was rescued from oblivion by several of his fellow botanists at the university who had knowledge of his long-sustained work. They were Irving B. McNulty, Robert K. Vickery, Kimball T. Harper, and Delbert Wiens. They obtained a grant from the University of Utah research committee for retyping and bringing the manuscript into final form. The latter task was largely the responsibility of Dr. Wiens, who was director of the University of Utah herbarium. The University of Utah Press declined to publish such a large and technical work, so it was submitted to the Brigham Young University Press, which accepted it. Thus, Dr. Flowers's work on the mosses of Utah came full circle back to BYU.

Not knowing of Dr. Crum's previous role and looking at the matter largely from a book-manufacturing viewpoint, authorities at the Brigham Young University Press, called upon Arthur Holmgren, the well-known botanist and expert on flowering plants at Utah State Unviersity, to edit the book. As previously noted, he was a student in the first class on mosses that Dr. Flowers taught at the University of Utah during the summer of 1935. In the preface he wrote Professor Holmgren commented that he was requested to reduce the manuscript by one-third, which was done largely by eliminating Dr. Flowers's long lists of citations of collections. It is also interesting to note that, with Professor Holmgren editing the book, all three of the universities in Utah had a role in the final production of this monumental work.

In his introduction Dr. Flowers sketched the history of bryology in Utah, noting the relatively few workers and their contributions and commented that this final work was based on 12,000 specimens gathered over a period of 47 years from nearly every part of Utah as well as bordering parts of neighboring states. The book was finally published in 1973 (Flowers 1973a). In the text 256 species are treated in 77 genera and 18 families. Many of these had been found to occur in Utah for the first time by Dr. Flowers. The book provides keys for identification of the kinds, gives detailed descriptions and illustrations, and discusses the geographical distribution and habitats occupied by each. The species accounts are accompanied by detailed observations by Dr. Flowers. Since the coverage of the text extends beyond Utah into contiguous areas, the book is essentially a guide to the mosses of the intermountain region. Dr. Steere prepared the foreword, commenting that one of the finest features of the book was the beautifully executed and original illustrations.

Once the book appeared in print, Dr. Crum undertook the task of segregating out the new forms described in the book and formalizing the descriptions. He explained that, although the descriptions had been prepared by Dr. Flowers and were fully illustrated in his book, the novelties presented therein required nomenclatural validation. Consequently, he assembled, organized, and paraphrased the descriptions and put them into Latin. The article that Dr. Crum thus prepared bore the name of Dr. Flowers as author (Flowers 1973b).

Regarding Dr. Flowers's other work on mosses, scrutiny of his bibliography shows several short notes that report new occurrences of certain species and several papers dealing with morphological features of different species. There was a series of eight reviews of sections of Dr. Grout's longtime project of presenting new material on mosses in a work that was called *North American Musci Perfecti.* Dr. Flowers prepared monographs or revisions of three natural groups of mosses, namely, the North American family Bartramiaceae (Flowers 1953d), the family Encalyptaceae (Flowers 1938a), and a worldwide revision of the genus *Anacolia* (Flowers 1925b). New species or varieties described prior to those in his book on the mosses of Utah were a new variety of *Encalypta ciliata* var. *pilifera* (Flowers 1946a) and a new species of *Tortula* from Utah and Arizona (Flowers 1951). A late contribution covered both the mosses and lichens in the Navajo National Monument in Arizona (Flowers 1963b).

Unpublished manuscripts on mosses found in his files were the "Mosses of the Deep Creek Mountains," a handwritten work containing a list of 9 species; "Pipe Springs Mosses," a similar short list; "A Synoptical Classification of Mosses" (8 pages); a 21-page mimeographed article pertaining to Drouet and Daly's revision of the Chroococcales, which he probably used in class work; and a 24-page typewritten catalog of mosses in his personal collection. The latter is incomplete.

In the preface he noted that the numbers up through 2,999 pertain to mosses from Utah, and subsequent numbers were used for mosses from North America at large. One obscure item pertains to a continuation of his early monograph on the family Bartramiaceae. If the writer recalls correctly from conversations with Dr. Flowers, there were only a few species remaining in connection with this work that needed clarification, but to work things out he would have had to visit European herbaria. This was a time when grant money was relatively easy to obtain from the National Science Foundation. The writer and his colleagues urged him repeatedly to make application for funds, but he couldn't be moved to do so. Apparently, he had lived too long at the bare subsistence level of support for his research, proceeding slowly largely by virtue of his personal effort. He couldn't seem to break away from his way of doing things. He didn't want the pressure to produce that a grant would bring. Another possible explanation was that he felt that his personal finances could not handle the additional extra expenses that would have inevitably resulted.

As regards the Hepaticae or liverworts, the other class of the Bryophyta, those kinds that he found in Utah were first discussed along with the mosses (Flowers 1936) in the paper on the bryophytes of Utah. Later (Flowers 1945), they were treated separately. Another summary came several years later (Flowers 1954a). The final comprehensive monograph appeared in 1961 (Flowers 1961b).

Similarly, the *Algae of Utah* went through several revisions, starting with a mimeographed descriptive catalog (Flowers 1938b) and followed by another more formal but still mimeographed version two years later (Flowers 1940a). Probably, had he lived long enough, this too would have resulted in a formal publication. Two unpublished manuscripts on algae found in his effects were a "Checklist of the Algae of the Glen Canyon Tributaries," an 8-page typewritten manuscript; and one on the "Algae of the Upper San Juan Basin," a 4-page handwritten product.

A large work evidently planned on the fungi of Utah seemingly never got beyond a 5-page handwritten and a 3-page typewritten "Index to Utah Fungi" found in his files. There is no indication of when this was compiled.

He worked assiduously on the lichens of Utah during all the years I knew him, collecting specimens at every opportunity. The results went through at least two versions. The first (Flowers 1952e) was a 30-page mimeographed *An Introduction to the Study of Lichens*, which he used in his classes. The second (Flowers 1954b) was a list of the lichens known to occur in Utah. A later study (Flowers 1963b) pertained to the lichen and moss flora of Betatakin Canyon and vicinity in Arizona. Found in his files was a 53-page catalog of lichens collected by Seville Flowers. They were taken mainly in Utah, but many were from surrounding states.

Second only to his work on mosses were his contributions on ferns and fern allies. His monumental resumé *Ferns of Utah* (Flowers 1944b) was antedated by a mimeographed manual on ferns issued in 1939, prepared, he said, "for use of nature study students." Later he described a new species of fern ally from southern Utah that he named *Selaginella utahensis* (Flowers 1949b, 1952a) and reported another fern occurring in the state (Flowers 1965b). An unpublished three-page mimeographed paper listing the ferns of Utah occurring in different life zones was found in his files, along with a longer paper entitled "The Genus *Selaginella* and Phylogeny and distribution of the Euselaginella of the *Selaginella rupestris* Group." This may have been the paper delivered before the Utah Academy of Sciences for which an abstract was published (Flowers 1952f). He went farther afield in studying ferns than for the other groups of plants since he studied the ferns of two nearby states. Results of his research on the ferns of Idaho appeared in three places. The first (Flowers 1949a) was a mimeographed leaflet issued by the daho State College herbarium. The second (Flowers 1950) was a list of the ferns of the state. The third was a summary of the Pteridophyta of Idaho (Flowers 1952d), which was part of the *Flora of Idaho* by Ray J. Davis. Apparently he was working on the ferns of Montana at the time of his death, and a mimeographed publication (Flowers 1967) on some ferns of Montana was issued by the University of Montana. As was true for nearly all his work, it was copiously illustrated with his original drawings showing structural features.

He devoted much time to the study of Utah grasses. Arthur Holmgren referred to his being an accomplished agrostologist. Again, had he lived long enough, a comprehensive formal summary paper would probably have been published. As it was, his *Common Grasses of Utah* went through two mimeographed versions. The first (Flowers 1943b) was a 104-page descriptive catalog with 50 plates. The second, revised edition (Flowers 1959b) had grown to 122 pages accompanied by dozens of illustrations.

As previously noted, one field in which Dr. Flowers had few peers was the microscopic identification of woods. His encouragement of one graduate student to work on this topic resulted in a joint publication (Saul and Flowers 1953). Found in Dr. Flowers' files was a two-page handwritten list of "Woods Native in Utah."

Side issues appeared in his research from time to time. One brief flurry saw a return to zoology, which he had taught in high school. He prepared two descriptive catalogs, *The Fishes of Utah* (1937d) and *The Amphibians of Utah* (1937e), both mimeographed. Probably, these were used in summer courses in field biology at the University of Utah. Another was a biography of Mary Parry Haines (Flowers 1942c), whose collection of mosses, hepatics, and lichens he had acquired. In this he gives an analysis of the material received. He published an article on the ethnobryology of the Gosiute Indians of Utah (Flowers 1957).

He was called upon to summarize the flora and fauna of Great Salt Lake for a book on saline lakes of the world. For this he enlisted the aid of Frederick R. Evans, who was studying the Protozoa in the lake (Flowers and Evans 1966). An item of interest in this connection is that Dr. Flowers had been culturing a strange amoeba from the lake brine for about a year, noting changes in the organism's appearance in different salt concentrations. A colleague, Dr. David T. Jones, became interested in the same problem, and Dr. Flowers graciously deferred to him. The new amoeba was named in 1944 after Dr. Flowers as *Amoeba flowersi* Jones (Univ. Utah Biol. Ser. 8(4):3).

A mimeographed teaching aid (Flowers 1965a), *An Introduction to Plant Classification*, went through at least two revisions. Dr. Flowers's (1968) history of cryptogamic botany was another long-sustained labor of love. He noticed that authors of botanical manuals often gave names to or attached brief accounts of plants mentioned by very early writers, some dating back to the Greek and Roman philosophers. Mostly the references were to the higher, flowering plants. He wondered what the early writers had had to say about the lower plants. So, over many years as he had occasion to visit large institutional libraries, he perused ancient herbals and copied quotations on cryptogams from original sources. Gradually he compiled a history of cryptogamic plants. A semi-popular discussion of fossil plants appeared in 1943 (Flowers 1943a).

In going through his research material following his death, Lois Arnow found three noteworthy unpublished manuscripts and teaching aids in addition to those detailed in the foregoing discussion of his research in certain specialty areas and the so-called side areas of research. Because of their informality, these have not been entered in the bibliography. One was a 6-page handwritten manuscript entitled "Notes on Halogeton," an introduced plant injurious to livestock. Another was a bibliography on fossil bryophytes (6 typewritten pages). The last was a treatment of the Compositae of Utah (99 unnumbered pages). One of Dr. Flowers's characteristics was planning for things far ahead, and, evidently, he intended to eventually concentrate on the composites. On what was perhaps his last field trip, Lois Arnow asked him what he was going to work on after his book *The Mosses of Utah* was published. His reply was that he wanted to do the Compositae of Utah.

During the last several years of his research career, Dr. Flowers's work turned in a new direction when he became affiliated with a developing program in ecology at the University of Utah. First came his association with the Dugway Proving Grounds' studies when the university entered into a contract with the U.S. Army to study the ecology of disease transmission in the remote desert region of western Utah in Tooele County. The first director was his colleague Dr. Angus M. Woodbury, who called upon Bill Flowers as a consultant to help plan the study of the plant aspects of the biotic communities of the area and to identify the vegetative types. He was admirably prepared for this assignment because of his prior doctoral study of the vegetation of the Great Salt Lake area. He delivered a paper (Flowers 1955) on ecological sample areas as standards for biotic communities at a symposium held at Dugway 6–8 August 1955. His list of plants of the region (Flowers 1956c) appeared in Dr. Woodbury's compilation of ecological checklists for the Great Salt Lake Desert.

At a later period, the University of Utah, largely through the efforts of Don M. Rees and A. M. Woodbury, contracted with the U.S. Bureau of Reclamation for a biological survey of the Glen Canyon, the most important aspect of which was an assessment of the riverine vegetation in relation to transpiration and water loss. Again, Dr. Woodbury headed the project and Dr. Flowers became the key man in conducting the plant studies and field inventories. Dr. Stephen D. Durrant had charge of the field operations and logistics. After a preliminary reconnaissance trip to the area in the autumn of 1957, in which Dr. Flowers participated, a checklist of plants was prepared by Cottam, Flowers, and Woodbury (1958). The intensive field study was made during the summer of 1958. For this Dr. Flowers prepared a key to the dominant trees and shrubs of the Glen Canyon silt region along the Colorado River for the aid of his field crews. This was a five-page mimeographed work. The final results of the study were presented in two reports. The first pertained to the overall survey of the vegetation of the Glen Canyon reservoir basin under the authorship of Woodbury, Durrant, and Flowers (1959). The second, more detailed report dealt with various ecological studies of the flora and fauna, under Dr. Woodbury's editorship, which contained Dr. Flowers's (1959b) account of the vegetation of the Glen Canyon.

The Glen Canyon survey was so successful that the university team was asked to conduct similar studies during the following summers at several other reservoir sites along the Upper Colorado River and its tributaries. For each study Dr. Flowers and numerous helpers, mostly students, handled the botanical studies. The Flaming Gorge Basin survey was conducted during the summer of 1959, with the main report being prepared by Woodbury, Durrant, and Flowers (1960) and the report on the vegetation by Flowers (1960). The Navajo Reservoir Basin was surveyed the next summer in 1960. Again the overall report was by Woodbury, Durrant, and Flowers (1961). In addition, there were reports on the vegetative aspects by Flowers (1961a) and Hall and Flowers (1961). The Curecanti Reservoir Basin was studied in 1961. Following precedent, the main report was by Woodbury, Durrant, and Flowers (1962). The botanical work had expanded somewhat with separate papers by Flowers (1962a), Flowers (1962b), and Hall and Flowers (1962).

At the conclusion of this series of studies on the Upper Colorado River, Dr. Woodbury arranged for an ecological study of the Dinosaur National Monument in Utah and Colorado. As before, Dr. Flowers was a principal member of the survey team. He prepared a paper (Flowers 1963a) on the nonvascular plants. Finally, there came the ecological survey of the Navajo National Monument in northern Arizona, including Betatakin Canyon. In this connection Dr. Flowers (1963b) summarized the data he collected on the lichen and moss flora of the area. It is possible that this Colorado River field work and subsequent report writing delayed much other planned research as well as the working up for final publication of several major projects, such as the algae and grasses of Utah. But Dr. Flowers gloried in the field work and the opportunity for collecting. Also there was the economic factor of extra income.

For several decades, starting in the 1930s, the team of Walter P. Cottam and Seville Flowers handled virtually all the botanical work at the University of Utah. The two complemented each other—Dr. Cottam with his emphasis on flowering plants and Dr. Flowers with his specialty area in cryptogamic botany. In many respects, besides their specialty areas, they were opposites. Dr. Cottam was the extrovert with public relations inclinations. He was a man of remarkable vision with a broad view of ecological problems affecting the welfare of mankind. In his teaching and research he dealt largely with the practical analysis and management of grazing resources. He was noted for his superb photography and fascinating illustrated lectures on flowering plants. He held offices in local professional societies and received much acclaim and many awards. In contrast, Dr. Flowers was more of an introvert. He was a retiring or reserved personality. He was content to work essentially alone in either of his laboratories, one at home, the other at the university, surrounded by specimens of plants, microscopic equipment, reference books, and manuscripts. He cared little for recognition. In his classroom teaching, he resorted to much "chalk talk," drawing illustrations on the blackboard. Both men were superb ecologists and zealous in field work, adding greatly to the university's herbarium. They were equally liked and respected by students and colleagues, each for his own virtues. Dr. Flowers was particularly appreciated for his thoroughness and orderly presentations in his lectures and for the teaching aids he prepared.

The long and distinguished career of Seville Flowers came to a sudden end at his home on the morning of 29 April 1968, two months short of his retirement from teaching. With hat and lunch bag in hand and on the verge of departing for his office at the university a few blocks away, he slumped to the kitchen floor from a massive heart attack. Funeral services were held at the church of his affiliation, St. Paul's Episcopal Church. A brief notice of his death, accompanied by his picture, appeared in the *Bryologist* (vol. 71:159. 1968). His friends and colleagues at the University of Utah placed a large rock with an affixed bronze plate on a grass-covered mound surrounded by small trees outside the biology building. The inscription reads "This memorial grove donated by students, friends, and colleagues of Dr. Seville Flowers, 1900–1968. Professor of Botany, 1936–1968. State Arboretum of Utah."

His personal collection of hepatics, mosses, and lichens had always been kept separate, never having been part of the university's herbarium. With the realization that work in his fields of specialization would not be continued at the university, where the entire biology area was undergoing the throes of redirection and reorganization along molecular and population biology lines, his wife and botany colleagues decided to place his technical books, separates, correspondence, specimens, and uncompleted manuscripts at some institution where active work was being done in his specialty areas. The recipient institution decided upon was the University of Colorado herbarium at Boulder, by arrangement with Dr. William Weber, director. Items were packed for transfer to Colorado by Dr. Weber, Dr. Wiens, and Lois Arnow, curator of the Garrett Herbarium. General books from his library went to the University of Utah. Thus passed from the scene a remarkably versatile and gifted individual who was a great scholar, a dedicated researcher, and an effective teacher. His numerous papers and monographs constitute evidence of his research productivity and the outstanding role that he played in the field of botany in Utah. Long after his death he was honored by a flowering plant in the family Scrophulariaceae being named after him—*Penstemon flowersii* Neese & Welsh (Great Basin Nat. 43[3]:429–431. 1983). In acknowledging his contributions the authors wrote: "The plant is named to honor the memory of Dr. Seville Flowers, late professor of botany at the University of Utah. Dr. Flowers was a student of lichens, mosses, and higher plants, and his untimely passing has left a void in the understanding of the plants of Utah and the West."

In this memorial I have stressed Dr. Flowers's writing and scientific achievements. It seems appropriate to conclude by reviewing his attributes as a teacher. It has been noted that a large part of his work load was instructing sections of the general education general biology course. His ability to illustrate principles by drawing on the blackboard was very effective. His popularity as a teacher at the lower-division level was indicated by his being invited along with his wife several times to "favorite professor" dinners and receptions conducted by sororities and other student groups. At the upper-division level he frequently requested that he be permitted to teach advanced or specialized courses. This was not so much for his own satisfaction as it was an accommodation for botany majors whom he felt needed the courses to round out their training. He never forgot his early experience of wanting to major in botany and finding few offerings. For these advanced courses he prepared the numerous handouts noted.

It was the consensus among majors and graduate students that he was an inspired and inspiring teacher. He was greatly appreciated for a trait that students expressed as "having heart," meaning that he had a deep feeling for students and the predicaments in which they found themselves. For example, a Ph.D. candidate of the writer had a botany minor and Dr. Flowers was a member of his committee to represent the area. Initially, the student failed the written botany qualifying examination. Dr. Flowers's high standards and sense of responsibility would not allow him to pass the student, yet he showed great discomfort at having to hold the student back another quarter. He actually seemed to rejoice when the student passed a different examination on the second round. Another student had "examination phobia." Dr. Flowers arranged for him to obtain credit for a course by a means other than taking the written examinations. Many times the comment appeared on student evaluation forms that Dr. Flowers always had time to answer questions in individual consultation. It is not an exaggeration to say that he was revered by many students. One girl was so emotionally overcome when she learned of his sudden death that she was unable to attend classes that day. Instead she went hiking in the mountains, where she felt she could reflect on the influence that he had had on her life.

Lois Arnow nicely summed up the teaching aspect of Dr. Flowers's career with the comment that "his quiet enthusiasm for the subjects he taught engendered interest where none might otherwise have existed. And he must have enjoyed teaching. For him teaching may have been a reason for being, especially in view of the many unpublished works prepared especially for students."

In the preparation of this memorial I have had the indispensable help of his widow, Emily Flowers, and of Lois Arnow. The manuscript was reviewed by both of them as well as by Kimball Harper, Irving B. McNulty, Robert K. Vickery, and Delbert Wiens, all of whom, like the writer, were his longtime associates, friends, and admirers. Their suggestions have greatly strengthened this memorial.

Bibiliography of Seville Flowers

1929. A preliminary list of Utah mosses. Bryologist 32:74–83.

1930. *Pottia randii* Kennedy. Bryologist 33:30.

1933a. On fossil mosses. Bryologist 36:26–27.

1933b. *Grimmia alpicola* var. *latifolia* Zett. Bryologist 36:27.

1933c. Mosses of the Great Salt Lake region. Bryologist 36:34–43.

1934. Vegetation of the Great Salt Lake region. Bot. Gazette 95:353–418.

1935a. Mosses of Utah (mimeographed). Published by the author. Price, Utah. 1–48, many illus.

1935b. Brood branches in *Philonotis*. Bryologist 38:8–9.

1935c. [Review of] A. J. Grout, North American Musci Perfecti, Nos. 276–300. Bryologist 38:115.

1935d. Family Bartramiacae. *In* A. J. Grout, Moss flora of North America north of Mexico. Vol. 2(3):152–179. Newfane, Vermont.

1936. The bryophytes of Utah. Bryologist 39:97–104.

1937a. [Review of] A. J. Grout, North American Musci Exsiccati, Nos. 301–325. Bryologist 40:64–66.

1937b. *Physcomitrium pygmaeum*. Bryologist 40:80.

1937c. A card index to the files of the Bryologist. Bryologist 40:113.

1937d. The fishes of Utah, a descriptive catalog (mimeographed). Univ. of Utah. 17 pp., 35 figs.

1937e. Amphibians of Utah (mimeographed). Univ. of Utah. 1–4, 13 figs.

1938a. Family Encalyptaceae. *In* A. J. Grout, Moss flora of North America north of Mexico. Vol. 1 (3):137–145, pls. 69–72. Newfane, Vermont.

1938b. Descriptive catalog of Utah algae (mimeographed). Univ. of Utah: 1–69, 37 figs.

1939. [Review of] A. J. Grout, North American Musci Perfecti, Nos. 326–350. Bryologist 42:83–84.

1940a. Common algae of Utah (mimeographed). Univ. of Utah: 1–70, many illus.

1940b. [Review of] A. J. Grout, North American Musci Perfecti, Nos. 351–375. Bryologist 43:172.

1941. [Review of] A. J. Grout, North American Musci Perfecti, Nos. 376–400. Bryologist 44:103–104.

1942a. [Review of] A. J. Grout, North American Musci Perfecti, Nos. 401–425. Bryologist 45:47–48.

1942b. Plant life of the Great Salt Lake region. News Bull. Mineral. Soc. Utah 3(2):36–56.

1942c. Mary Parry Haines, 1826–1884. Proc. Indiana Acad. Sci. 51:78–82.

1943a. Fossil plants. News Bull. Mineral. Soc. Utah 4(2):35–50, 8 figs.

1943b. Common grasses of Utah, a descriptive catalog (mimeographed). Univ. of Utah 104 pp., 50 pls.

1944a. [Review of] A. J. Grout, North American Musci Perfecti, Nos. 426–450. Bryologist 47:46–47.

1944b. Ferns of Utah. Univ. of Utah Bull. 35(7), Biol. Ser. 4(6):1–87, 164 figs.

1945. Utah hepatics. Bryologist 48:8–11.

1945. The Bryophyte herbarium: a moss collection: preparation and care. (H. S. Conard, S. Flowers, P. M. Patterson, and F. E. Wynne.) Bryologist 48:198–202. [Report of a Committee of the Sullivant Moss Society]

1946a. *Encalypta ciliata* var. *pilifera* n. var. Bryologist 49:84.

1946b. [Review of] A. J. Grout, North American Musci Perfecti, Nos. 451–475, 210A and 393A. Bryologist 49:87.

1947. A visit with Dr. Grout. Bryologist 50:208–212.

1949a. Contribution toward a flora of Idaho: Pteridophytes (mimeographed). Idaho State College Herbarium Leaflet No. 27: 1–37.

1949b. A new *Selaginella* from southwestern Utah. Amer. Fern Jour. 39:83–86.

1950. A list of the ferns of Idaho. Amer. Fern Jour. 40:121–131.

1951. A new species of *Tortula* from Utah and Arizona. Bryologist 54:278–282.

1952a. Additional notes on *Selaginella utahensis*. Amer. Fern Jour. 42:58–60.

1952b. Monograph of the genus *Anacolia*. Bull. Torrey Bot. Club 79:161–185.

1952c. Two Crossidiums in Utah. Bryologist 55:216–218.

1952d. [Subkingdom Pteridophyta, ferns and fern allies]. Pages 29–62 *in* Ray J. Davis, Flora of Idaho. William C. Brown, Dubuque, Iowa.

1952e. An introduction to the study of lichens (mimeographed). Univ. of Utah: 1–30, 39 figs.

1952f. Distribution and relationships of the *Euselaginellae* [Abstract]. Proc. Utah Acad. Sci., Arts, and Lett. 30:109–110.

1953. *Tortula papillosissima*, new to North America. Bryologist 56:160–164.

1953. The identification of woody shrubs of Utah based on stem anatomy. (W. E. Saul, and S. Flowers.) Proc. Utah Acad. Sci., Arts, and Lett. 30:30–31.

1954a. Liverworts of Utah. Proc. Utah Acad. Sci., Arts, and Lett. 31:93–100.

1954b. Some lichens of Utah. Proc. Utah Acad. Sci., Arts, and Lett. 31:101–105.

1955. Ecological sample areas as standards for biotic communities. Pages 11–12 *in* Symposium on Ecology of Disease Transmission in Native Animals. Dugway Proving Grounds April 6–8, 1955.

1956a. *Dicranoweisia crispula* and *D. cirrhata*. Bryologist 59:239–244.

1956b. New methods of cutting sections of moss stems and leaves. Bryologist 59:244–246.

1956c. Plants. Pages 115–125 *in* A. M. Woodbury, ed., Ecology of the Great Salt Lake Desert: ecological check lists. Univ. of Utah Ecological Research, The Great Salt Lake Desert series.

1957. Ethnobryology of the Gosiute Indians of Utah. Bryologist 60:11–14.

1958. Check list of plants. (W. P. Cottam, S. Flowers and A. M. Woodbury.) Pages 42–123 *in* Preliminary report on biological resources of the Glen Canyon reservoir. Univ. of Utah Anthropological Papers No. 31 (Glen Canyon Ser. No. 2).

1959. Survey of vegetation in the Glen Canyon reservoir basin. (A. M. Woodbury, S. D. Durrant, and S. Flowers). Univ. of Utah Anthropological Papers No. 36 (Glen Canyon Ser. No. 5): vi + 1–53.

1959a. Vegetation of Glen Canyon. Pages 21–61 *in* Ecological studies of the flora and fauna in Glen Canyon. Univ. of Utah Anthropological Papers No. 40 (Glen Canyon Ser. No. 7).

1959b. Common grasses of Utah, rev. ed. (mimeographed). Univ. of Utah: 1–122, many illus.

1960. A survey of vegetation in the Flaming Gorge reservoir basin. (A. M. Woodbury, S. D. Durrant, and S. Flowers.) Univ. of Utah Anthropological Papers No. 45 (Upper Colorado Ser. No. 2): vii + 1–121.

1960. Vegetation of Flaming Gorge reservoir basin. Pages 1–98 *in* Ecological studies of the flora and fauna of Flaming Gorge reservoir basin, Utah and Wyoming. Univ. of Utah Anthropological Papers No. 48 (Upper Colorado Ser. No. 3).

1961. A survey of vegetation (A. M. Woodbury, S. D. Durrant, and S. Flowers.) Univ. of Utah Anthropological Papers No. 51 (Upper Colorado Ser. No. 4): vii + 1–99.

1961a. Vegetation of the Navajo reservoir basin in Colorado and New Mexico, 1960. Pages 15–46 *in* Ecological studies of the flora and fauna of the Navajo reservoir basin, Colorado and New Mexico. Univ. of Utah Anthropological Papers No. 55 (Upper Colorado Ser. No. 5).

1961b. The Hepaticae of Utah. Univ. of Utah Biol. Ser. 12(2):1–89, 18 pl.

1961. Vascular plants found in the Navajo reservoir basin, 1960, Colorado and New Mexico. (H. H. Hall, and S. Flowers.) Pages 47–87 *in* Ecological studies of the flora and fauna of the Navajo reservoir basin, Colorado and New Mexico. Univ. of Utah Anthropological Papers No. 55 (Upper Colorado Ser. No. 5).

1962. A survey of vegetation in the Curecanti reservoir basins. (A. M. Woodbury, S. D. Durrant, and S. Flowers.) Univ. of Utah Anthropological Papers No. 56 (Upper Colorado Ser. No. 6): viii + 1–98.

1962a. Vegetation of Morrow Point and Blue Mesa reservoir basins of the upper Gunnison River, Colorado. Pages 12–46 *in* Ecological studies of the flora and fauna of the Curecanti reservoir basins, western Colorado. Univ. of Utah Anthropological Papers No. 59 (Upper Colorado Ser. No. 8).

1962b. Plants found in Curecanti Reservoir basins, 1961: nonvascular plants. Pages 47–51 *in* Ecological studies of the flora and fauna of the Curecanti reservoir basins, western Colorado. Univ. of Utah Anthropological Papers No. 59 (Upper Colorado Ser. No. 8).

1962. Plants found in Curecanti Reservoir basins, 1961: vascular plants (except grasses). (H. H. Hall, and S. Flowers.) Pages 52–91 *in* Ecological studies of the flora and fauna of the Curecanti reservoir basins, western Colorado. Univ. of Utah Anthropological Papers No. 59 (Upper Colorado Ser. No. 8).

1963a. Study of non-vascular plants, Dinosaur National Monument. Univ. of Utah Div. Biol. Sci. Misc. Papers No. 1: 49–68.

1963b. The lichen and moss flora of Betatakin Canyon and vicinity, Navajo National Monument, Arizona. Univ. of Utah Div. Biol. Sci. Misc. Papers No. 3:1–10.

1965a. Introduction to plant classification (mimeographed). Univ. of Utah: 1–85.

1965b. *Asplenium resiliens* in Utah. Amer. Fern Jour. 55:142–143.

1965c. The 1964 foray of the American Bryological Society in Colorado. Bryologist 68:246–250.

1966. The flora and fauna of the Great Salt Lake region, Utah. (S. Flowers, and F. R. Evans.) Pages 367–393 *in* Hugo Boyko, ed., Salinity and aridity. Dr. W. Junk, Publishers. The Hague.

1967. Some ferns of Montana (mimeographed). Univ. of Montana: 1–37, 157 figs.

1968. A brief history of Cryptogamic botany (mimeographed). Univ. of Utah: 1–88.

1973a. Mosses: Utah and the West. Brigham Young University Printing Service, Provo. Edited by Arthur Holmgren with foreword by William C. Steere. 567 pp.

1973b. Mosses of Utah new to science. Bryologist 76:286–292. Edited by and descriptions put into Latin by Howard Crum.

NEW GENERIC SYNONYMY AND NEW GENERA OF SCOLYTIDAE (COLEOPTERA)

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Abstract.— New generic synonymy in Scolytidae is proposed as follows: *Amasa* Lea (=*Pseudoxyleborus* Eggers), *Araptus* Eichhoff (=*Brachydendrulus* Schedl, *Gnathocranus* Schedl, *Gnathoborus* Schedl), *Chortastus* Schaufuss (=*Afrochramesus* Schedl), *Cosmoderes* Eichhoff (=*Dendriops* Schedl), *Cryphalus* Erichson (=*Acryphalus* Tsai & Li, *Jugocryphalus* Tsai & Li), *Cyrtogenius* Strohmeyer (=*Eulepiops* Schedl, *Ozodendron* Schedl, *Mimidendrulus* Schedl, *Artepityophthorus* Schedl), *Dendrographus* Schedl (=*Protopityophthorus* Schedl), *Glostatus* Schedl (=*Paraglostatus* Schedl), *Gnathotrupes* Schedl (=*Gnathocortus* Schedl, *Gnathomimus* Schedl, *Gnathoglochinus* Schedl), *Hylesinopsis* Eggers (=*Metahylesinus* Eggers, *Hapalophloeus* Schedl, *Hemihylesinus* Schedl), *Hypothenemus* Westwood (=*Chondronoderes* Schedl, *Archeophalus* Schedl, *Pachynoderes* Schedl, *Lepiceroides* Schedl), *Liparthrum* Wollaston (=*Dacryophthorus* Schedl), *Mimiocurus* Schedl (=*Micracidendron* Schedl, *Mimiophthorus* Schedl), *Miocryphalus* Schedl (=*Afromicracis* Schedl), *Phloeoditica* Schedl (=*Xylechinops* Browne), *Pityophthorus* Eichhoff (=*Breviophthorus* Schedl, *Neomips* Schedl), *Pseudothysanoes* Blackman (=*Bostrichips* Schedl, *Gretschkinia* Sokanovskii, *Neoglostatus* Schedl), *Scolytodes* Ferrari (=*Hexacolinus* Schedl, *Cryphalophilus* Schedl), *Scolytogenes* Eichhoff (=*Xylocryptus* Schedl), *Taphrorychus* Eichhoff (=*Saliciphilus* Sokanovskii, *Taphroterus* Schedl), *Tricolus* Blandford (=*Pterocyclonoides* Schedl), *Triotemnus* Wollaston (=*Cladoproctus* Schedl), *Xylosandrus* Reitter (=*Apoxyleborus* Wood). New specific synonymy in Scolytidae is proposed for: *Chortastus agnatus* Eggers (=*Afromicracis baguenai* Schedl), *Pelicerus* (now *Dendrographus*) *pygmaeus* Eggers (=*Protopityophthorus durus* Schedl). The status of *Pseudomicracus* Eggers is discussed. The following new genera are proposed in Scolytidae: *Phloeographus* (type-species: *Phloeographus mamibiae* Wood), *Phloeocurus* (type-species: *Hylocurus africanus* Schedl), *Saurotocis* (type-species: *Micracidendron tomicoides* Schedl), and *Peridryocoetes* (type-species: *Ozodendron nitens* Schedl). *Pseudothysanoes spinatulus*, new name, is proposed to replace *P. spinatus* Wood, 1956.

Over the past five years a reclassification of the genera of Scolytidae in world fauna has been in progress. During this period, I have had opportunities to visit and study the collections of K. E. Schedl, Y. Niisima, J. J. Murayama, A. Nobuchi, C. F. C. Beeson, and others, and to examine through loan the type-specimens of the type-species of most of the named genera and subgenera of Scolytidae. To stabilize nomenclature for the generic study and to make names on identified specimens comprehensible to curators, the generic synonymy summarized in the above abstract is proposed on the following pages. Assigned to synonymy are 43 genera and subgenera that represent scolytid taxa from all inhabited continents of the world. Two species (one in *Chortastus* from Africa, and one in *Dendrographus* from New Guinea) were also placed in synonymy, because they were type-species of monobasic genera that were placed in synonymy. Synonymy affecting numerous other species will follow in subsequent papers. Four genera are named as new to science, as indicated in the above abstract.

New Synonymy

Amasa Lea

Amasa Lea, 1894, Proc. Linn. Soc. New South Wales (2) 8:322 (Type species: *Amasa thoracicus* Lea = *Tomicus truncatus* Erichson, monobasic)

Pseudoxyleborus Eggers, 1930, Indian For. Rec. 14:206 (Type species: *Pseudoxyleborus beesoni* Eggers, monobasic). *New synonymy*

In the Schedl collection more than 25 species had been assigned by Schedl to the *truncatus* Erichson and *beesoni* Eggers species groups. These two groups had been combined by him into one group. After studying his material and seeing complete integradation between the two, I now agree that the genera *Amasa* Lea and *Pseudoxyleborus* Eggers must be combined under the senior name as indicated above.

Araptus Eichhoff

Araptus Eichhoff, 1892, Berliner Ent. Zeitschr. 15:136 (Type-species: *Araptus rufopalliatus* Eichhoff, monobasic)

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Brachydendrulus Schedl, 1951, Dusenia 2:114 (Type-species: *Brachydendrulus eggersi* Schedl, monobasic). *New synonymy*

Gnathocranus Schedl, 1951, Dusenia 2:116 (Type-species: *Gnathocranus novateutonicus* Schedl, monobasic). *New synonymy*

Gnathoborus Schedl, 1970, Koleopt. Runschau 48:93 (Type-species: *Breviophthorus argentiniae* Schedl, original designation). *New synonymy*

The large, diverse genus *Araptus* Eichhoff is represented in the Schedl collection by limited material in only a few species groups. My examination of the type series, including the types, of *Brachydendrulus eggersi* Schedl, *Gnathocranus novateutonicus* Schedl, and *Breviophthorus argentiniae* Schedl (type-species of the genus *Gnathoborus*) all fall well within the limits of *Araptus*. For this reason, the genera *Brachydendrulus* Schedl, *Gnathocranus* Schedl, and *Gnathoborus* Schedl must all be placed in synonymy under the senior name *Araptus*, as indicated above.

Chortasus Schaufuss

Chortastus Schaufuss, 1905, Insekten Borse 22:15 (Type-species: *Chortastus camerunus* Schaufuss, monobasic)

Afrochramesus Schedl, 1971, Koleopt. Rundschau 49:197 (Type-species: *Afromicracis baguenai* Schedl, original designation). *New synonymy*

The paratype of *Afrochramesus baguenai* Schedl in the Schedl collection and a cotype of *Chortastus agnatus* Eggers in the Schedl collection are essentially identical and obviously are of the same species. On the basis of this comparison, *Afromicracis* is placed in synonymy under *Chortastus*, to which both belong.

Cosmoderes Eichhoff

Cosmoderes Eichhoff, 1878, preprint of Mem. Soc. Roy. Sci. Liege (2) 8:495 (Type-species: *Cosmoderes monilicollis* Eichhoff, monobasic)

Dendriops Schedl, 1953, Rev. Franc. d'Ent. 20:125 (Type-species: *Dendriops granulicollis* Schedl, monobasic). *New synonymy*

The identity of *Cosmoderes monilicollis* Eichhoff was established by Wood (1980, Great Basin Nat. 40:91), although the type is lost. Examples of this species were compared directly to the lectotype of *Dendriops granulicollis* Schedl and were found to be congeneric. Because these species are the type-species of their respective genera, the name *Dendriops* must be placed in synonymy as indicated above.

Cryphalus Erichson

Cryphalus Erichson, 1836, Archiv Naturgesch. 2(1):61 (Type-species: *Bostrichus asperatus* Gyllenhal, designated by Thompson 1859:147)

Acryphalus Tsai & Li, 1963, Acta Ent. Sinica 12:604, 662 (Type-species: *Cryphalus lipingensis* Tsai & Li, present designation). *New synonymy*

Jugocryphalus Tsai & Li, 1963, Acta Ent. Sinica 12:602,622 (Type-species: *Cryphalus piceus* Eggers, present designation). *New synonymy*

The subgenus *Acryphalus* Tsai & Li was proposed to include *Cryphalus lipingensis* Tsai & Li, *C. markangensis* Tsai & Li, and *C. lepocrinus* Tsai & Li, but a type species was not designated. I here designate *C. lipingensis* as the type-species of *Acryphalus*. I have examined a series of this species that was identified by Prof. Yin Hui-fen, who had access to the holotype. This subgenus was based on the absence or near absence of elytral scales. This is not a valid or reliable character in this genus. For this reason, *Acryphalus* is placed in synonymy as indicated above.

The subgenus *Jugocryphalus* Tsai & Li was based on the presence of a transverse carina on the male vertex. Assigned to this *subgenus* were *Cryphalus tabulaeformis* Tsai & Li (and its subspecies *chienzhaungensis* Tsai & Li), *C. pseudochinlingensis* Tsai & Li, *C. chinlingensis* Tsai & Li, *C. piceus* Eggers, *C. massonianus* Tsai & Li, *C. jeholensis* Murayama, *C. fulvus* Niisima, *C. pseudotabulaeformis* Tsai & Li, *C. szechuanensis* Tsai & Li (and its subspecies *tehchanzensis* Tsai & Li), *C. exiguus* Blandford, and *C. mandschuricus* Eggers. Because a type-species was not designated, I here designate *Cryphalus piceus* Eggers as the type-species of *Jugocryphalus*. The name *Ericryphalus* Hopkins was based on the same character and would have priority if a subgeneric name is needed for this group of species. The name *Jugocryphalus* is placed in synonymy under *Cryphalus* as indicated above.

Cyrtogenius Strohmeyer

Cyrtogenius Strohmeyer, 1910, Ent. Blätt. 6:127 (Type-species: *Cyrtogenius bicolor* Strohmeyer, monobasic)

Eulepiops Schedl, 1939, J. Fed. Malay St. Mus. 18:344 (Type-species: *Eulepiops glaber* Schedl, original designation). *New synonymy*

Ozodendron Schedl, 1957, Ann. Mus. Roy. Congo Belge (8) Sci. Zool. 56:13 (Type-species: *Pelicerus grandis* Beeson, monobasic). *New synonymy*

Mimidendrulus Schedl, 1957, Ann. Mus. Roy. Congo Belge (8), Sci. Zool. 56:68 (Type-species: *Mimidendrulus movoliae* Schedl, monobasic. *New synonymy*

Artepityophthorus Schedl, 1969, Opusc. Zool. Budapest 9:157 (Type-species: *Artepityophthorus aries* Schedl, monobasic). *New synonymy*

The holotypes of *Eulepiops glaber* Schedl, *Pelicerus grandis* Beeson, *Mimidendrulus movoliae* Schedl, and *Artepityophthorus aries* Schedl were examined. These are the type-species of *Eulepiops* Schedl, *Ozodendron* Schedl, *Mimidendrulus* Schedl, and *Artepityophthorus* Schedl. All these species fall well within the limits of *Cyrtogenius* Strohmeyer and are here placed in synonymy. Schedl (1961, Rev. Ent. Mocambique 4(2):752) listed as the type-species of *Mimidendrulus* a species not included in that monobasic genus when it was erected. His oversight must be ignored.

Among the smaller species of *Cyrtogenius* there is an orderly reduction in the number of segments in the antennal funicle from four to three. Schedl used this character (three segments) to establish his genus *Artepityophthorus*, but placed several other species with a 3- or 4-segmented funicle *Cyrtogenius*. This reduction in segmentation is continued to two in *Dendrographus*, but other characters may warrant the continued recognition of a separate genus for that species (*D. pygmaeus* Eggers).

Schedl repeatedly called attention to the intergradation of the smaller *Cyrtogenius* to *Pityophthorus*; however, none of the species he cites exhibit any of the essential characters of that subtribe (Corthylini, Pityophthorina).

Dendrographus Schedl

Dendrographus Schedl, 1964, Reichenbachia 3:310 (Type-species: *Pelicerus pygmaeus* Eggers, original designation)

Protopityophthorus Schedl, 1973, Papua New Guinea Agric. J. 24:73 (Type-species: *Protopityophthorus durus* Schedl = *Pelicerus pygmaeus* Eggers, original designation). *New generic and specific synonymy*

Several cotypes of *Pelicerus pygmaeus* Eggers were examined and compared directly to my series that in turn was compared to the holotype and several paratypes of *Protopityophthorus durus* Schedl. They are identical. Except for the 2-segmented antennal funicle and slightly different club, this species would be placed in the genus *Cyrtogenius*. The future discovery of species that bridge this character gap may require suppression of *Dendrographus*.

Glostatus Schedl

Glostatus Schedl, 1939, Rev. Zool. Bot. Afr. 32:386 (Type-species: *Glostatus declividepressus* Schedl, monobasic)

Paraglostatus Schedl, 1964, Reichenbachia 3:304 (Type-species: *Ctonocryphus nigrivestis* Schedl, original designation). *New synonymy*

The holotype and several paratypes of *Ctonocryphus nigrivestitus* Schedl were examined. Because this species is a normal member of the genus *Glostatus* and because it was made the type-species of *Paraglostatus* Schedl, *Paraglostatus* must be placed in synonymy as indicated above.

Gnathotrupes Schedl

Gnathotrupes Schedl, 1951, Dusenia 2:123 (Type-species: *Gnathotrupes bolivianus* Schedl, monobasic)

Gnathocortus Schedl, 1975, Studies in the Neotropical Fauna 10:11 (Type-species: *Gnathocortus caliculus* Schedl, original designation). *New synonymy*

Gnathomimus Schedl, 1975, Studies in the Neotropical Fauna 10:12 (Type-species: *Gnathomimus nothofagi* Schedl, original designation). *New synonymy*

Gnathoglochinus Schedl, 1975, Studies in the Neotropical Fauna 10:16 (Type-species: *Gnathoglochinus impressus* Schedl, original designation). *New synonymy*

Schedl named *Gnathocortus*, *Gnathomimus*, and *Gnathoglochinus*, each based on the type-species cited above, from limited material, apparently without reviewing the South American species he had previously placed in *Gnathotrupes* and (erroneously) *Gnathotrichus*. These and several manuscript genera (*Gnathostractus*, *Gnathoxylene*, *Eidognathus*) all represent minor variations of *Gnathotrupes*. The three named genera are here placed in synonymy, as indicated above.

Hylesinopsis Eggers

Hylesinopsis Eggers, 1920, Ent. Blätt. 16:40 (Type-species: *Hylesinopsis dubius* Eggers, monobasic)

Metahylesinus Eggers, 1922, Ent. Blätt. 18:165 (Type-species: *Pseudohylesinus togonus* Eggers, automatic). *New synonymy*

Hapalophloeus Schedl, 1966, Rev. Ent. Moçambique 8:363 (Type-species: *Metahylesinus brinckei* Schedl, original designation). *New synonymy*

Hemihylesinus Schedl, 1967, Opusc. Zool. Budapest 7:224 (Type-species: *Hemihylesinus endroedyi* Schedl, monobasic). *New synonymy*

A significant number of species scattered in six or more genera in the Schedl collection all represent the same genus. Included among them are the type-species, as cited above, for the genera *Hylesinopsis* Eggers, *Metahylesinus* Eggers, *Hapalophloeus* Schedl, and *Hemihylesinus* Schedl. Following a careful review, it was concluded that segmentation of the antennal funicle, characters of the antennal club, body vestiture, and other features used to characterize genera, were so variable that the group could not be divided into definable units. Consequently, the names *Metahylesinus*, *Hapalophloeus*, and *Hemihylesinus* are here placed in synonymy as indicated above.

Hypothenemus Westwood

Hypothenemus Westwood, 1836, Trans. Ent. Soc. London 1:34 (Type-species: *Hypothenemus eruditus* Westwood, monobasic)

Chondronoderes Schedl, 1940, Mitt. Münchner Ent. Ges. 30:589 (Type-species: *Stephanoderes magnus* Eggers, monobasic). *New synonymy*

Archeophalus Schedl, 1941, Rev. Zool. Bot. Afr. 34:392 (Type-species: *Archeophalus natalensis* Schedl, monobasic). *New synonymy*

Pachynoderes Schedl, 1941, Rev. Zool. Bot. Afr. 34:393 (Type-species: *Pachynoderes deprecator* Schedl, monobasic). *New synonymy*

Lepiceroides Schedl, 1957, Ann. Mus. Roy. Congo Belge (8) Sci. Zool. 56:59 (Type-species: *Lepiceroides aterrimus* Schedl, monobasic). *New synonymy*

Cotypes and metatypes of *Stephanoderes magnus* Eggers, holotypes of *Archeophalus natalensis* Schedl and *Pachynoderes deprecator* Schedl, and more than a dozen paratypes of *Lepiceroides atterrimus* Schedl were examined. All are clearly congeneric with *Hypothenemus eruditus* Westwood. Because these species are the type-species of *Chondronoderes* Schedl, *Archeophalus* Schedl, *Pachynoderes* Schedl, *Lepiceroides* Schedl, and *Hypothenemus* Westwood, the four junior names must be placed in synonymy under the senior name as indicated above.

Liparthrum Wollaston

Liparthrum Wollaston, 1854, Insecta Maderensia, p. 294 (Type-species: *Liparthrum bituberculatum* Wollaston, original designation)

Dacryophthorus Schedl, 1971, Ent. Scand. Suppl. 1:281 (Type-species: *Dacryophthorus brincki* Schedl, original designation). *New synonymy*

Two paratypes of *Dacryophthorus brincki* Schedl are identical to a series of this species taken in Ceylon by me. This species quite clearly is a member of the genus *Liparthrum* Wollaston in both anatomical and biological characters. The pubescent, shallowly impressed female frons of this species is widely shared by tropical species of this genus. *Dacryophthorus* is here placed in synonymy under the senior name as indicated above.

Mimiocurus Schedl

Mimiocurus Schedl, 1957, Ann. Mus. Roy. Congo Belge (8) Sci. Zool. 56:72 (Type-species: *Mimiocurus acuminatus* Schedl, monobasic)

Micracidendron Schedl, 1957, Ann. Mus. Roy. Congo Belge (8) Sci. Zool. 56:71 (Type-species: *Micracidendron montanum* Schedl, monobasic). *New synonymy*

Mimiophthorus Schedl, 1957, Ann. Mus. Roy. Congo Belge (8) Sci. Zool. 56:77 (Type-species: *Brachydendrulus congonus* Schedl, original (?) or subsequent designation). *New synonymy*

Schedl (1957) designated "*Brachydendrulus montanus Schedl*" as the type-species of *Mimiophthorus*. Because no such species had been named, it is presumed that this was a mental error that was corrected when he later listed *Brachydendrulus congonus* Schedl (1962, Rev. Ent. Moçambique 5(1):63) as the type-species of *Mimiophthorus*. A review of five paratypes of *B. congonus*, 24 of *Mimiocurus acuminatus* Schedl, and 14 of *Micracidendron montanum* Schedl indicates that all belong to the same genus. Because each of these three species is the type-species of a generic name, *Micracidendron* and *Mimiophthorus* are placed in synonymy under *Mimiocurus* by choice of the first revisor. The genus was placed in Ipini by Schedl; however, it quite clearly is a member of the subtribe Pityophthorina (Corthylini).

Miocryphalus Schedl

Miocryphalus Schedl, 1939, Rev. Zool. Bot. Afr. 32:381 (Type-species: *Stephanoderes natalensis* Eggers, monobasic)

Afromicracis Schedl, 1959, Ann. Mag. Nat. Hist. (13) 1:709 (Type-species: *Afromicracis kenyaensis* Schedl, monobasic). *New synonymy*

A female cotype of *Stephanoderes natalensis* Eggers was compared to four paratypes of *Afromicracis kenyaensis* Schedl and to the types of six other species assigned by Schedl to *Miocryphalus*. Because all represent the same genus, the junior generic name, *Afromicracis*, must be placed in synonymy as indicated above.

Phloeoditica Schedl

Phloeoditica Schedl, 1962, Verhandl. Naturf. Ges. Basel 73:189 (Type-species: *Kissophagus curtus* Eggers, present designation)

Xylechinops Browne, 1973, Rev. Zool. Bot. Afr. 87:283 (Type-species: *Xylechinus australis* Schedl, original designation). *New synonymy*

A cotype of *Kissophagus curtus* Eggers was compared directly to long series of this species from India and adjacent areas; they are clearly conspecific. This species was also compared to and is congeneric with several other species including *Xylechinus australis* Schedl (five paratypes examined). Because *K. curtus* is the type-species of *Phloeoditica* Schedl and is congeneric with *X. australis*, type-species of *Xylechinops* Browne, the latter generic name must be placed in synonymy as indicated above.

Pityophthorus Eichhoff

Pityophthorus Eichhoff, 1864, Berliner Ent. Zeitschr., 8:39 (Type-species: *Bostrichus lichtensteini* Ratzeburg, subsequent designation by Hopkins 1914)

Breviophthorus Schedl, 1938, Archiv Naturgesch. 7:176 (Type-species: *Breviophthorus brasiliensis* Schedl, monobasic). *New synonymy*

Neomips Schedl, 1954, Dusenia 5:37 (Type-species: *Neomips brasiliensis* Schedl, monobasic). *New synonymy*

The holotype and a series of other specimens of *Breviophthorus brasiliensis* Schedl were examined and compared to numerous neotropical *Pityophthorus* species. While *B. brasiliensis* is in a recognizable species group, I see no characters that suggest it might be a distinct genus from 20 or more other, equally distinct species groups. For this reason, *Breviophthorus* is placed in synonymy under *Pityophthorus*.

Schedl named *Neomips brasiliensis* from male specimens that superficially resemble certain *Acanthotomicus* species. The female is an average member of neotropical *Pityophthorus*. The only deviant feature of *Neomips* is the male elytral declivity. I do not regard this as adequate justification to characterize a genus and, consequently, place *Neomips* in synonymy as indicated above.

The transfer of *Beviophthorus brasiliensis* Schedl, 1938, and *Neomips brasiliensis* Schedl, 1954, to *Pityophthorus* creates homonymy. The younger name (1954) is replaced by its junior synonym *P. dimorphus* Schedl.

Pseudomicracis Eggers

Pseudomicracis Eggers, 1920, Ent. Blätt. 16:36 (Type-species: *Pseudomicracis elsae* Eggers, original designation)

The unique holotype of *Pseudomicracis elsae* Eggers is lost. A careful study of the original description and of all African Micracini having strongly procurved antennal sutures and the elytral apex mucronate drastically limits the number of species that could fit into this genus. Although *P. elsae* obviously has not been rediscovered, several named species seem to meet all the character requirements of this genus. All the African (including Madagascar) species placed by Schedl in *Micracis* lack the strongly flattened protibia, with the socketed teeth on the apical margin. The African *Micracis* have a more slender tibia and teeth on the apical portion of the lateral margin. The eye is oval and they share other minor characters not found in American *Micracis*. These African species appear to share all the significant generic characters of *P. elsae*. For this reason, I here transfer to *Pseudomicracis* the following species: *Hylocurus bugekeae* Schedl 1957 (Congo), *Micracis difficilis* Schedl 1965, *M. harunganae* Schedl 1961, *M. ignotus* Schedl 1965, *M. madagascarensis* Schedl 1961, and *M. pennatus* Schedl 1965 (all from Madagascar). With these transfers, the genera *Hylocurus* and *Micracis* are once again limited to the American continents.

Pseudothysanoes Blackman

Pseudothysanoes Blackman, 1920, Mississippi Agric. Expt. Sta. Bull. 9:46 (Type-species: *Pseudothysanoes drakei* Blackman = *Cryphalus rigidus* LeConte, original designation)

Bostrichips Schedl, 1951, Rev. Chilena de Ent. 1:21 (Type-species: *Bostrichips spinatus* Schedl, monobasic). *New synonymy*

Gretschkinia Sokanovskii, 1959, Ceskoslov. Spolec. Ent. Casopie 56:276 (Type-species: *Gretschkinia mongolica* Sokanovskii, monobasic). *New synonymy*

Neoglostatus Schedl, 1978, Ent. Abh. Mus. Tierk. Dresden 41:300 (1977) (Type-species: *Neoglostatus squamosus* Schedl, monobasic). *New synonymy*

Bostrichips spinatus Schedl, *Gretschkinia mongolica* Sokanovskii, and *Neoglostatus squamosus* Schedl are the type-species of the genus in which each was named. Cotypes and other specimens of *G. mongolica* and the holotypes and species related to the other two were examined and compared to numerous species of *Pseudothysanoes* Blackman. All three fall well within the limits of *Pseudothysanoes* and are here placed in synonymy under that name.

The transfer of *Bostrichus spinatus* Schedl, 1951, to *Pseudothysanoes* causes *P. spinatus* Wood, 1956, to become a junior homonym. The new name *Pseudothysanoes spinatulus* is proposed as a replacement for this junior homonym.

Scolytodes Ferrari

Scolytodes Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 77 (Type-species: *Scolytodes laevigatus* Ferrari, monobasic)

Hexacolinus Schedl, 1963, Reichenbachia 1:217 (Type-species: *Hexacolinus minutissimus* Schedl 1963 = *Scolytodes minutissimus* Schedl 1952, original designation). *New synonymy*

Cryphalophilus Schedl, 1970, Kontyu 38:358 (Type-species: *Cryphalophilus afer* Schedl, monobasic). *New synonymy*

The female holotypes of *Scolytodes minutissimus* Schedl and of *Hexacolinus minutissimus* Schedl were compared directly to one another and to my material. Only one species is represented. Because *Hexacolinus minutissimus* is the type-species of the genus in which it was named, *Hexacolinus* is here placed in synonymy as indicated above. The name *H. minutissimus* is both a junior homonym and a junior synonym and is automatically replaced.

The five paratypes of *Cryphalophilus afer* Schedl clearly fall within the limits of *Scolytodes*. Because *C. afer* is the type-species of that genus, *Cryphalophilus* Schedl is here placed in synonymy as indicated.

Scolytogenes Eichhoff

Scolytogenes Eichhoff, 1878, preprint of Mem. Soc. Roy. Sci. Liege (2) 8:475, 479 (Type-species: *Scolytogenes darwini* Eichhoff, monobasic)

Xylocryptus Schedl, 1975, Ann. Naturhistor. Mus. Wien 79:352 (Type-species: *Xylocryptus papuanus* Schedl, original designation). *New synonymy*

The genus *Scolytogenes* Eichhoff is a large and moderately diverse tropical genus that inhabits a variety of vines (creepers) and related plants. The type-species, *S. darwini* Eichhoff, based on the holotype in the Schedl collection is one of the most highly evolved and widely distributed species in the genus. The more primitive members of the genus are small and have antennae resembling those of *Eidophelus* Eichhoff species. *Xylocryptus papuanus* Schedl is one of several New Guinea species in the more primitive section of *Scolytogenes*. Because *X. papuanus* falls well within the limits of this genus, it is here placed in synonymy as indicated above.

Taphrorychus Eichhoff

Taphrorychus Eichhoff, 1878, preprint of Mem. Soc. Roy. Sci. Liege (2)8:49, 204 (Type-species: *Bostrichus bicolor* Herbst, subsequent designation by Hopkins 1914)

Saliciphilus Sokanovskii, 1954, Byull. Mosk. O. I. P. (Biol.) 59:17, 20 (Type-species: *Hypothenemus machnovskii* Sokanovskii, original designation). *New synonymy*

Taphroterus Schedl, 1965, Ann. Hist. Nat. Mus. Nat. Hungarici 57:341 (Type-species: *Taphroteres primitus* Schedl, monobasic). *New synonymy*

Two paratypes of *Hypothenemus machnovskii* Sokanovskii in my collection have been studied and pondered for many years. After examining two additional paratypes in the Schedl collection, I now agree with Schedl (private notes) that this species should be placed in *Taphrorychus*. Because *H. machnovskii* is the type-species of the generic name *Saliciphilus*, this genus must be placed in synonymy as indicated above.

Also in the Schedl collection is one paratype of *Taphroterus primitus* Schedl, type-species of the genus in which it was named. This species is allied to the three Japanese species named by Murayama and is here transferred to *Taphorychus*. This transfer of its type-species requires that *Taphroterus* be placed in synonymy as indicated above.

Tricolus Blandford

Tricolus Blandford, 1905, Biol. Centr. Amer., Coleopt. 4(6):286 (Type-species: *Tricolus ovicollis* Blandford, subsequent designation by Hopkins 1914)

Pterocyclonoides Schedl, 1970, Koleopt. Rundschau 48:101 (Type-species: *Pterocyclonoides octodentatus* Schedl, monobasic). *New synonymy*

The unique holotype of *Pterocyclonoides octodentatus* Schedl was examined. It is a small, very slender member of the genus *Tricolus* and is allied to other Brazilian members of that genus. Because it is the type-species of *Pterocyclonoides*, this transfer requires that the junior generic name be placed in synonymy as indicated above.

Triotemnus Wollaston

Triotemnus Wollaston, 1864, Catalog Coleopt. Canaries, p. 264 (Type-species: *Triotemnus subretusus* Wollaston, monobasic)

Cladoctoporcus Schedl, 1975, Rev. suisse Zool. 82:454 (Type-species: *Cladoctoporcus scrofa* Schedl, original designation). *New synonymy*

Two paratypes of *Cladoctoporcus scrofa* Schedl and a diagram in the Schedl collection of the holotype indicate that this species is an average member of the genus *Triotemnus* Wollaston. I find no characters not also represented in other members of this genus and note that Schedl erroneously reversed the sexes. The generic transfer of the type-species requires that the name *Cladoctoporcus* be placed in synonymy as indicated above.

Xylosandrus Reitter

Xylosandrus Reitter, 1913, Wiener Ent. Zeit. 32 (Beiheft):80, 83 (Type-species *Xyleborus morigerus* Blandford, monobasic)

Apoxyleborus Wood, 1980, Great Basin Nat. 40:90 (Type-species: *Xyleborus mancus* Blandford, original designation). *New synonymy*

After examining in the Schedl collection several hundred species of Xyleborini not previously known to me, my concept of the genus *Xylosandrus* Reitter has changed slightly. *Xyleborus mancus* Blandford, type-species of *Apoxyleborus* Wood, is here transferred to *Xylosandrus* and my generic name is placed in synonymy as indicated.

Xylosandrus and *Censtus* Sampson are much larger than previously supposed and may intergrade. Much more study will be required to determine the extent and reliability of the apparent character gap that separates them.

NEW TAXA

Phloeographus, n. gen.

This genus is allied to *Polygraphus* Erichson, but is distinguished by the two slightly procurved sutures on the antennal club, by the emarginate eye, and by the *Tomicus*-like elytral declivity. Additional generic characters are incorporated into the description of the type-species.

Type-species: *Phloeographus mamibiae*, n. sp.

Phloeographus mamibiae, n. sp.

This species resembles primitive *Polygraphus* species except as noted.

FEMALE.— Length 2.2 mm; proportions not measured but body about 2.4 to 2.6 times as long as wide; color dark brown.

Frons shallowly concave from eye to eye from epistoma to vertex; densely punctured and ornamented by short, dense pile, marginal setae very long. Eye emarginate. Antennal funicle 5-segmented, club moderately asymmetrical and acuminate as in *Polygraphus*, with two clearly marked, slightly procurved, aseptate sutures. Scutellum not visible. Pronotum and elytra about as in *Tomicus* but slightly resembling *Polygraphus*; strial punctures in rows, punctures small, impressed; interstriae almost smooth, with fine, uniseriate punctures, each bearing a row of short, uniseriate scales toward declivity. Declivity about as in *Tomicus*, with interstriae 2 weakly impressed, 1 and 3 each with a row of about five small tubercles.

HOLOTYPE.— The unique female holotype is labeled: "S. W. Afr., Damara, Farm Bethanis, 20.25 S-14-24E; 17-2-1978; E-Y:673, grassnetting, leg. Endrody and Schulze." The specimen bears a Schedl label indicating that he made a microscope slide mount of one antenna and a label bearing the manuscript name *Halytes mamibiae*.

The holotype is in the Naturhistorisches Museum Wien, Austria.

Saurotocis, n. gen.

As indicated above, *Micracidendron montanum* Schedl was tranferred to the genus *Mimiocurus* of the Corthylini. However, the other two species that were placed in *Micracidendron* by Schedl, *tomicoides* Schedl and *dispar* Schedl, belong to a new genus of Micracini that is described as follows.

DESCRIPTION.— Eye short, oval, entire. Antennal club 2.0 or more times as long as wide, covered by dense, fine, short pubescence, entirely unmarked by sutures. Protibia slender, with three socketed teeth on outer apical margin as in *Pseudothysanoes*. Elytral apex acuminate, mucronate; female declivity simple, male somewhat impressed medially, lateral areas elevated and remarkably ornamented by spines.

Type-species: *Micracidendron tomicoides* Schedl.

Phloeocurus, n. gen.

Schedl (1957, Ann. Mag. Nat. Hist. (12)10:875) named *Hylocurus africanus*, a phloeophagous species, in a xylophagous genus not previously known to occur in Africa. My examination of most of the type series indicates that this species belongs to a new genus that is described as follows.

Description.— Eyes entire, finely faceted, elongate, 2.5–3.0 times as long as wide. Female frons convex. Protibia more or less cylindrical, with socketed denticles on apical margin, not armed on posterior face by tubercles. Antennal club with two moderately procurved sutures marked by rows of setae. Elytral apex acuminate and somewhat mucronate; declivity convex, armed by moderately coarse tubercles in both sexes. Phloeophagous.

Type species: *Hylocurus africanus* Schedl.

Peridryocoetes, n. gen.

Schedl (1964, J. Australian Ent. Soc. 11:146) cites, without giving names, the assignment of three species to *Peridryocoetes* and names *queenslandi* in this genus, although it is not congeneric with the other three. A search of his collection and of the catalog of types in his collection (Schedl, 1979, Kataloge der wissenschaftlichen Sammlungen des Naturhistorischen Museums in Wien, Entomologie, Band 3, heft 2, 286 p.) indicates that the three original species were *Ozodendron nitens* Schedl, *Xyleborus peliciformis* Schedl, and *Dryocoetes minutissimus* Schedl. However, searches of his published papers and of major indexes to taxonomic literature did not locate a description or other validation of the generic name. Because a name is needed for my review of the genera of Scolytidae, this genus is described here.

The genus *Peridryocoetes* is distinguished from *Cyrtogenius* and *Dryocoetes* by characters of the body form, antennal club, pronotum, and elytra as described below.

Description.— Body stout, 2.0–2.1 times as long as wide. Pronotum uniformly asperate to base, with no punctures indicated; summit on basal fourth. Antennal club either without sutures or with suture 1 on basal fourth; this suture almost straight, except recurved at margins. Procoxae narrowly separated. Elytral declivity convex, strongly arched, apical fourth exceeding vertical and undercutting median area at and near apex.

Type-species: *Ozodendron nitens* Schedl.

ECOLOGICAL STUDIES OF A REGULATED STREAM: HUNTINGTON RIVER, EMERY COUNTY, UTAH

Robert N. Winget[1]

ABSTRACT.— A 36.9×10^6 m^3 reservoir constructed on Huntington River, Emery County, Utah, resulted in changes in physical habitat, water quality, temperature, and flow regime. The greatest changes in physical habitat resulted from: (1) sediment additions from dam and road construction plus erosion of reservoir basin during filling; and (2) changing stream flow from a spring high runoff regime to a moderated flow regime. Elimination of spring nutrient concentration peaks and overall reduction of total dissolved nutrient availability in the river plus moderate reductions in pH were the most apparent water quality changes below the reservoir. Water temperature changes were an increased diurnal and seasonal constancy, summer depression, and winter elevation, generally limited to a 10–12 km reach below the dam.

Physical and chemical changes altered macroinvertebrate community structure, with changes greatest near the dam and progessively less as distance downstream increased. Below the dam: (1) more environmentally tolerant taxa increased their dominance; (2) relative numbers of smaller sized individuals increased in relation to larger individuals; and (3) filter feeding, collector/gatherers, and scrapers gained an advantage over shredders. Insect taxa such as *Rhithrogena robusta*, *Pteronarcella badia*, and *Ephemerella doddsi* were eliminated from stream reaches near the dam, and other taxa such as *Arctopsyche grandis*, Chironomidae, and Simuliidae increased in numbers. Late spring to early summer egg hatch proved to be a disadvantage to *Brachycentrus occidentalis*, and *B. americanus*, with a fall hatch, was less impacted by altered river flow patterns. Macroinvertebrate taxa with small instar larvae present from late summer to early fall were negatively impacted by the unnaturally high July and August flows. The reservoir became a physical barrier to downstream larval drift and upcanyon and downcanyon immigration of adults, resulting in reduced numbers of several species above and below the reservoir.

Huntington Canyon, approximately 890 square km drainage, lies along the eastern slope of the Wasatch Plateau in Emery County, east central Utah (Fig. 1), and is part of the Colorado River drainage. Huntington River originates in the Manti–LaSal National Forest at an elevation of about 3000 m and flows 83 km to the southeast to its confluence with the San Rafael River. Precipitation in the upper canyon (75–100 cm annually) comes primarily from winter snows. In the lower regions of the canyon, precipitation (30 cm) mainly comes in the form of high-intensity summer thunderstorms.

Two 430-megawatt, coal-fired electric generating units have been built by Utah Power and Light Company near the mouth of Huntington Canyon. To provide water for the plant, a 36.9×10^6 m^3 (30,000 ac-ft) reservoir was constructed on Huntington River 32 km upstream (Fig. 1). The reservoir (Electric Lake) began to fill the fall of 1973. Since then, river flows and water temperature and quality have been altered below the dam. As stated by Ward and Stanford (1979), "the river continuum . . . is profoundly interrupted when dams are employed by man to impound or divert river flow." The resultant effects of these changes on Huntington River macroinvertebrates were the major concern of this study.

Most impoundment related impacts on receiving streams can be classified into seven basic types: (1) nutrients and fine sediments from reservoir basins being washed downstream (mainly in new impoundments), (2) addition of plankton to downstream reaches, (3) discharge of sediment-free water from the reservoir, (4) alteration of natural water temperature regimes, (5) alteration of natural flow regimes, (6) water chemistry changes created by the impoundment, and (7) obstacles to primary macroinvertebrate recolonization mechanisms.

Although an effort may be made to remove organic materials from new reservoir basins before filling (trees, brush, and grasses), soils still contain quantities of soluble and small

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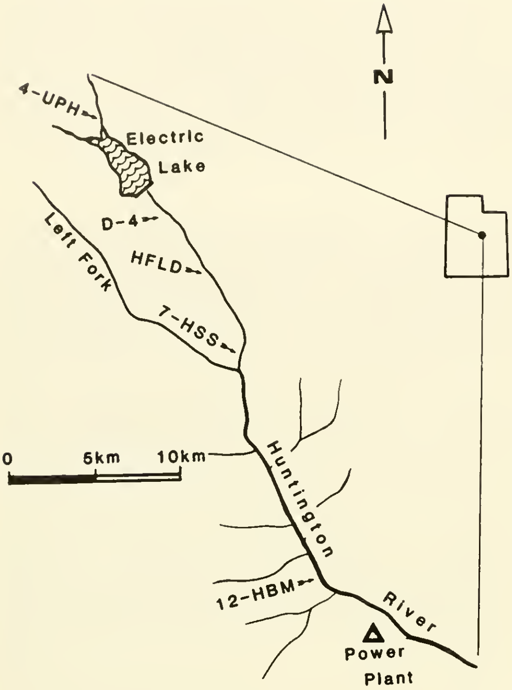

Fig. 1. Huntington River drainage showing location of Electric Lake Reservoir, the Huntington Power Generating Station, and study sampling stations.

particulate nutrients. These nutrients enter reservoir waters during filling and flow from the reservoir with release water. Silts produced during construction, in combination with nutrients from the impoundment in release waters, can cause increased algal growth below a dam (Mulligan and Baranowski 1969). Spence and Hynes (1971) noted that plankton from an impoundment often produced a macroinvertebrate community composition in the receiving stream like that found in streams affected by moderate organic enrichment. Increased epilithic algae below impoundments can result from clarifying effects of the reservoir, stabilization of substrates, increased nutrients, and higher water temperatures (Lowe 1979, Ward 1976a). Barber and Kevern (1973) found that increases in periphyton density decreased water current, with a corresponding deposition of fine sediments and detrital materials. These mats of algae can act as additional habitat, trapping detrital material and forming false bottoms (Pfitzer 1954), offering considerable shelter from the current and providing abundant food supply for some macroinvertebrates (Spence and Hynes 1971).

In a study on the North and South forks of the Anna River in Virginia, Kondratieff and Voshell (1981) indicated that low winter river water temperatures persisted longer into the summer, and warmer summer temperatures persisted longer into the fall in the impounded than in the unimpounded river. Ward (1976b) reported that some insects cannot lay eggs when temperatures are low, and eggs of others will not develop without cold temperatures. Eggs of some mayfly species must be subjected to near freezing temperatures before hatching (Lehmkuhl 1972). Altered temperatures can cause development and emergence to occur earlier or later than they would naturally (Coutant 1968, Nebeker 1971, Lillenammer 1975).

Rivers have distinct natural flow regimes depending on several factors, including the size of the area being drained, when and how much precipitation falls, and when and how fast snow melts, etc. Aquatic life is accustomed to, and even benefits from, natural flow regimes found in nature. Insects avoid natural spring runoff stresses by burrowing into the substrate, emerging as adults prior to runoff, or seeking slower portions of the river. They have adapted to the natural high and low flow patterns found in rivers. If, however, a large release was made "out of season" with high water velocity and accompanying sediment movements, fragile emerging adults could be killed before leaving the stream, early instar larvae could be covered with sediments and smothered, or sediments could interfer with feeding behavior. But if normal high flows are eliminated, sediments and algal growth would be allowed to build up from year to year, covering a major portion of available substrates (Ward 1974).

If macroinvertebrate species are eliminated from a stream reach by a short-term perturbation, recolonization is usually quick. This is accomplished by: (1) immatures drifting downstream from upstream unimpacted reaches, (2) adults immigrating to the impacted area and depositing eggs (adults could come from upstream or downstream), and (3) immatures crawling into the area from downstream. Drift recolonization is apparently the most important of the three recolonization mechanisms. Drift was shown by Gore (1979) to recolonize a newly openned river channel reach in 120 days. Bishop and Hynes (in Gore 1979) estimated that upstream migration accounts for only about 6.5% of the recolonization in a natural stream community. In a study made by Hilsenhoff (1971) of a newly dammed stream in Wisconsin, some insects did not appear in the community below the dam for two years after they were eliminated. Apparently, elimination of drift by an impoundment slows recolonization of the impoundment downstream. Large impoundments can interfer with downstream drift of immatures and adult immigration both up canyon and down.

Methods

This report presents a summary of the results of studies at five stations on Huntington River, one above Electric Lake (Station 4-UPH) and four stations below the lake (Stations D-4, HFLD, 7-HSS, 12-HBM) (Fig. 1). Station 4-UPH is located between Swens and Burnout Canyons approximately 10 km above Electric Lake Dam at an elevation of 2620 m. This station was not affected by dam construction, but construction of a youth camp 5 km upstream added sedimentation and organic enrichment during 1976 to 1978. Station D-4 is located 2 km below Electric Lake Dam at an elevation of 2530 m. Station HFLD, located 7 km below Electric Lake Dam at an elevation of 2470 m, was established in 1978 to describe sediment movement downstream. Station 7-HSS is located 13 km downstream from Electric Lake Dam at an elevation of 2410 m. Station 12-HBM is located approximately 32 km downstream from Electric Lake Dam at an elevation of 2010 m and 1.7 km above the Huntington Canyon Generating Station.

Water quality data used in this report were obtained from: (1) water quality samples collected and analyzed by the Environmental Analysis Laboratory, Brigham Young University, (2) a water quality monitoring program conducted by Vaughn Hansen Associates, Salt Lake City, Utah, and (3) on-going water quality monitoring by the Bureau of Reclamation, USDI. Algal bioassays were conducted by Porcella and Merritt (1976). Bioassay test conditions were generally equivalent to EPA procedures (EPA 1971). Several constant temperature Ryan thermographs were placed in selected sites on Huntington River during the 1971–74 period. Temperatures were measured during winter, spring, and summer months. All stream discharge values were taken from USGS and UP&L gauging station records. Results are presented as daily and monthly mean cfs discharges.

Three to four sediment samples per station per date were taken from potential trout-spawning gravel beds using a 15.24 cm diameter steel cylinder sampler similar to the one described by McNeil and Ahnell (1964). Samples were generally taken during early spring, midsummer, amd late fall each year, with extra samples taken in relation to increased discharges from Electric Lake. Sediments were dried and then separated into specified size classes: gravel (>4.75 mm diameter), coarse sand (2.0–4.7 mm), medium sand (0.5–1.99 mm), fine sand (0.075–0.49 mm), and silt/clay (<0.074 mm) (Cummins 1962). The total amount <0.85 mm is referred to as total fines at each station.

Macroinvertebrate samples were taken with a Surber Sampler (Surber 1937) modified by Winget (Fig. 2). The modified sampler was designed with a larger collecting bag, to prevent backwash when collecting in deep water, and 280-um mesh netting to collect small instar larvae. Samples were taken using the stratified random method (Weber 1973) with rubble substrate in riffles as selected habitat. Four samples per station per date were collected, fulfilling guidelines given by Elliott (1971). In the field, each sample was washed into a plastic dish pan and covered with a saturated sodium chloride (NaCl) solution (specific gravity 1.19), which caused macroinvertebrates and organic debris to float above the inorganic sediments (Rees and Winget 1970). Floating organic material was poured off through a 250-um mesh sieve (Tyler equivalent 60 mesh), placed in a labeled bottle, and preserved in 10% formalin solution.

At the laboratory, samples were divided into eight equal parts using a subsampler (Waters, 1969). Two to four subsamples, depending on the estimated total number of

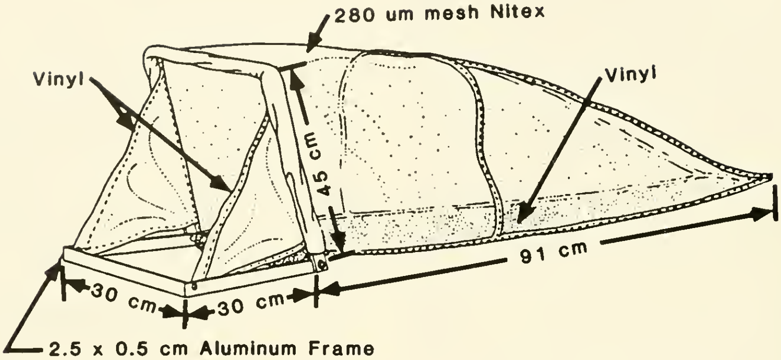

Fig. 2. Surber sampling device as modified by R. N. Winget in 1971.

insects in the sample, were randomly selected for processing. The remainder of the sample was preserved for later reference. Organisms were sorted to taxonomic groups, identified and counted, and body lengths of selected taxa were measured in mm, not counting antennae or cerci length (length measurements were used to define life histories). Organisms were dried for 8–10 hours at 80 C and then weighed to the nearest 0.1 mg. Data were analyzed for total, and by taxon densities and biomass, and community dominance diversity (H by Shannon and Weaver). Beginning in 1978, taxon (TQ) and community (CTQa and CTQd) tolerance quotients (Winget and Mangum 1979, and Winget 1984b) were calculated.

Results And Discussion

Water Quality

Before Electric Lake began filling, bicarbonate alkalinity in Huntington River generally had an annual cycle with values 175–250 mg/l from the first of August through the beginning of runoff in April or May; as runoff increased, alkalinity decreased until at peak runoff it was only 125–150 mg/l; and as runoff decreased through June and July, alkalinity gradually increased again. With Electric Lake and the moderated flows, alakalinity levels have had less seasonal fluctuation, with lows corresponding to high reservoir discharges rather than spring runoff. Bicarbonate alkalinity average concentrations during 1971–1973 (preimpoundment) and 1974–1979 (impoundment) were 145–179 and 154–216 mg/l, respectively.

The pH of Huntington River waters before Electric Lake generally ranged from 7.5 to 8.8, with lower values during winter/spring and higher values during summer/fall. Average pH for 1971–1973 was 8.3–8.5 at all stations. Huntington River is a bicarbonate-buffered stream accounting for the small pH changes recorded. After Electric Lake began to fill, pH of waters entering Huntington River from the reservoir were 7.0–8.3, with 7.0–7.6 being the most common. Moving downstream, pH soon increased to near preimpoundment values. For the period 1974–79, pH averaged 8.1 above Electric Lake (Station 4-UPH), 7.5 at the dam outfall, 7.8 at Station D-4 (2 km below the dam), 8.0 at Station 7-HSS (13 km below the dam), and 8.2 at Station 12-HBM (32 km below the dam).

Specific conductance was highly variable and increased downstream. Yearly average conductivities above Electric Lake ranged from 230 to 280 umhos/cm, 249 to 346 at the outlet, 317 to 470 at Station 7-HSS, and 334 to 519 at Station 12-HBM. Annual mean sulfate concentrations at Stations 4-UPH and 12-HBM were approximately 5 mg/l and 13.4 mg/l, respectively.

Nutrients in Huntington River, represented as nitrate nitrogen and ortho-phosphate, underwent significant changes in relation to Electric Lake. Before Electric Lake, both nitrate and ortho-phosphate concentrations increased with spring snowmelt. Dissolved nutrients from litter decomposition were

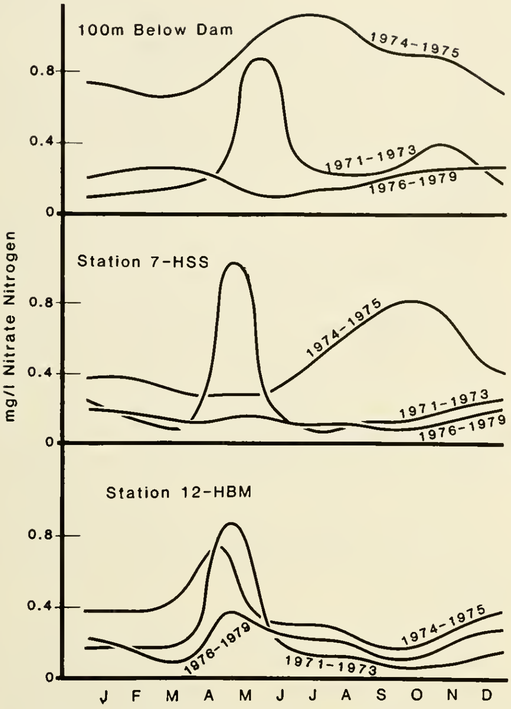

Fig. 3. Average nitrate concentrations for 1971–73 (preimpoundment), 1974–75 (initial filling period), and 1976–79 (impounded) at three stations on Huntington River.

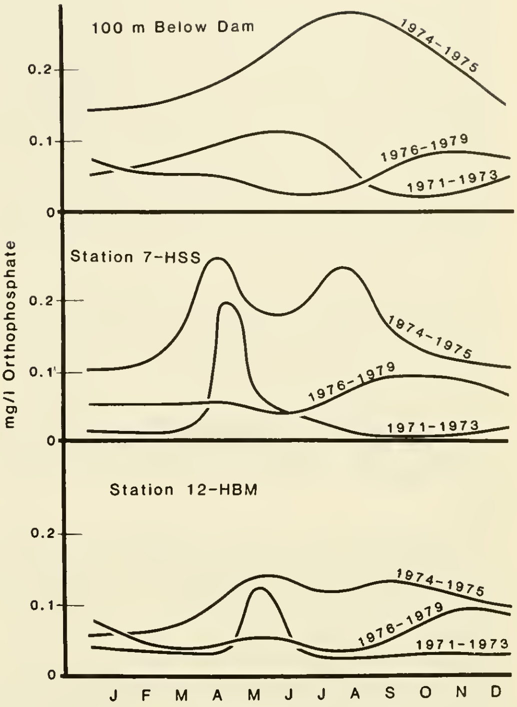

Fig. 4. Average ortho-phosphate concentrations for 1971–73 (preimpoundment), 1974–75 (initial reservoir filling period), and 1976–79 (impounded) at three stations on Huntington River.

carried into the stream with surface snowmelt, causing April–June peaks in concentration (Figs. 3 and 4). Borman and Likens (1979) found that plant communities accumulate nutrients and some salts in a plant-soil reservoir, and removal of the plant cover results in increases in concentration of nutrients and salts in surface runoff waters. During the 1974–75 period, following clear cutting of trees within the basin, waters began to cover exposed soils. Leaching of nutrients and salts was rapid, and increased ortho-phosphate and nitrate nitrogen levels were obvious below Electric Lake downstream to Station 7-HSS. Biological removal in the stream plus dilution with Left Fork waters lowered concentrations so that at Station 12-HBM increases were not evident.

Hannan (1979), in a review of chemical modifications in reservoir-regulated streams, reported that biological nutrient depletion within reservoirs is common. During the 1976–19 period nitrate nitrogen levels were lower than preimpoundment years at all stations below the reservoir (Fig. 3). Huntington River is nutrient poor, so biological activity within the reservoir readily captured most of the nutrients entering the system, resulting in low levels of dissolved nutrients in discharge waters. Ortho-phosphate concentration changes were similar to nitrate nitrogen, except ortho-phosphate showed a greater increase during fall overturn of Electric Lake than did nitrate nitrogen.

Results of a bioassay test of Huntington River and Electric Lake water illustrated the nutrient-poor nature of these waters. Samples for bioassay were taken from Huntington River at Station 4-UPH and from the reservoir surface near the dam in early August 1976. Chemical tests indicated phosphorus (P) levels in both samples at growth-limiting concentrations. Ratios of total inorganic nitrogen (N) to total P were 65 at inlet and 376 at site 1, indicating P strongly limiting relative to N (N/P>15 indicates P deficiency and N/P<15 indicates N deficiency). Bioassay results were essentially the same for the two samples. The samples responded to P alone and N plus P but not to N alone or trace elements (T.E.) alone. Essentially no growth occurred in either sample alone, thus verifying the low P levels measured chemically. Although nitrogen and phosphorus are generally considered the most important limiting nutrients for aquatic ecosystem primary productivity, based on biogeochemical reasoning (Hutchinson 1973), carbon dioxide is also often limiting. Carbon dioxide was not considered limiting because it can be taken from the abundant bicarbonates in Electric Lake and Huntington River. The geology of drainage basins in the Huntington Canyon area indicates that insolubility of trace elements might make them also limiting in some cases.

Dissolved oxygen (DO) in Huntington River most frequently ranges between 8 and 11 mg/l. Annual average DO for most stations was 8–10 mg/l. In 1974, the average DO measured above Electric Lake was 10.3 mg/l, compared with 7.8 at the dam outlet, and 9.8 at Station D-4. Dissolved oxygen concentrations react quickly to the turbulent flows in Huntington River and low water temperatures; thus concentrations were near saturation within a few km below the dam.

Water Temperature

Reservoirs can alter downstream water temperatures in several ways: (1) increased diurnal constancy, (2) increased seasonal constancy, (3) summer depression, (4) summer elevation, (5) winter elevation, and (6) thermal pattern changes (Ward and Stanford 1979). Thermal changes in Huntington River are of increased diurnal and seasonal constancy, summer depression, and winter elevation.

Changes in water temperature at the Electric Lake outlet were less dramatic compared with preimpoundment water temperatures, but in response to environmental stimuli, water temperatures returned to near preimpoundment ranges within a short distance downstream. Factors such as solar radiation, air temperature, water turbulance (channel morphology), amount of flow (reservoir discharge), turbidity, and TDS all affect a stream's rate of water temperature adjustment to "*normal.*" *Normal* refers to the temperature the water would be without the reservoir, or under natural conditions.

Before Electric Lake (1971–1972), diurnal summer fluctuations often spanned 10 C, but in winter and during peak runoff, diurnal fluctuations seldom exceeded 3 C (Fig. 5). Before Electric Lake, seasonal fluctuations at the dam site were 18–20 C, but after dam completion (1974) they were only 4–5 C. Winter water temperatures (December) at the outlet were 4–5 C higher in 1974 than in 1972, compared with only 1–2 C 2 km downstream. Spring temperatures (June) were 5–7 C lower in 1974 than in 1972 at the outlet, compared with only 3–4 C 2 km downstream. The greatest difference was during the summer, when Electric Lake discharge waters were 3–14 C cooler than stream water temperatures before Electric Lake. This compares with a difference of 3–8 C 2 km downstream.

By the time Huntington River waters reached station 7-HSS, 13 km below Electric Lake, water temperatures had nearly equilibrated with environmental factors (Fig. 5). There were no noticeable differences between pre- and postimpoundment water temperatures. Direct thermal impacts to biota from Electric Lake are likely limited to a 3–5 km reach of stream below Electric Lake. Because of downstream drift behavior of macroinvertebrates, the actual impact may extend considerably further downstream. Evidence discussed later indicates that in Huntington River thermal impacts on stream biota are rather minor when compared to impacts from flow modification and sedimentation.

Sedimentation

No measurements of stream sediments in Huntington River were made prior to spring 1974. Because of this, some basic assumptions have been made: (1) measurements made at Station 4-UPH above Electric Lake represent a close approximation of sediment characteristics in the vicinity of Electric Lake Dam (Station D-4) before construction (1971); and (2) sediment composition during 1975 at Station 7-HSS represented relatively unimpacted conditions, reflecting preimpoundment sediment conditions below Electric Lake Dam.

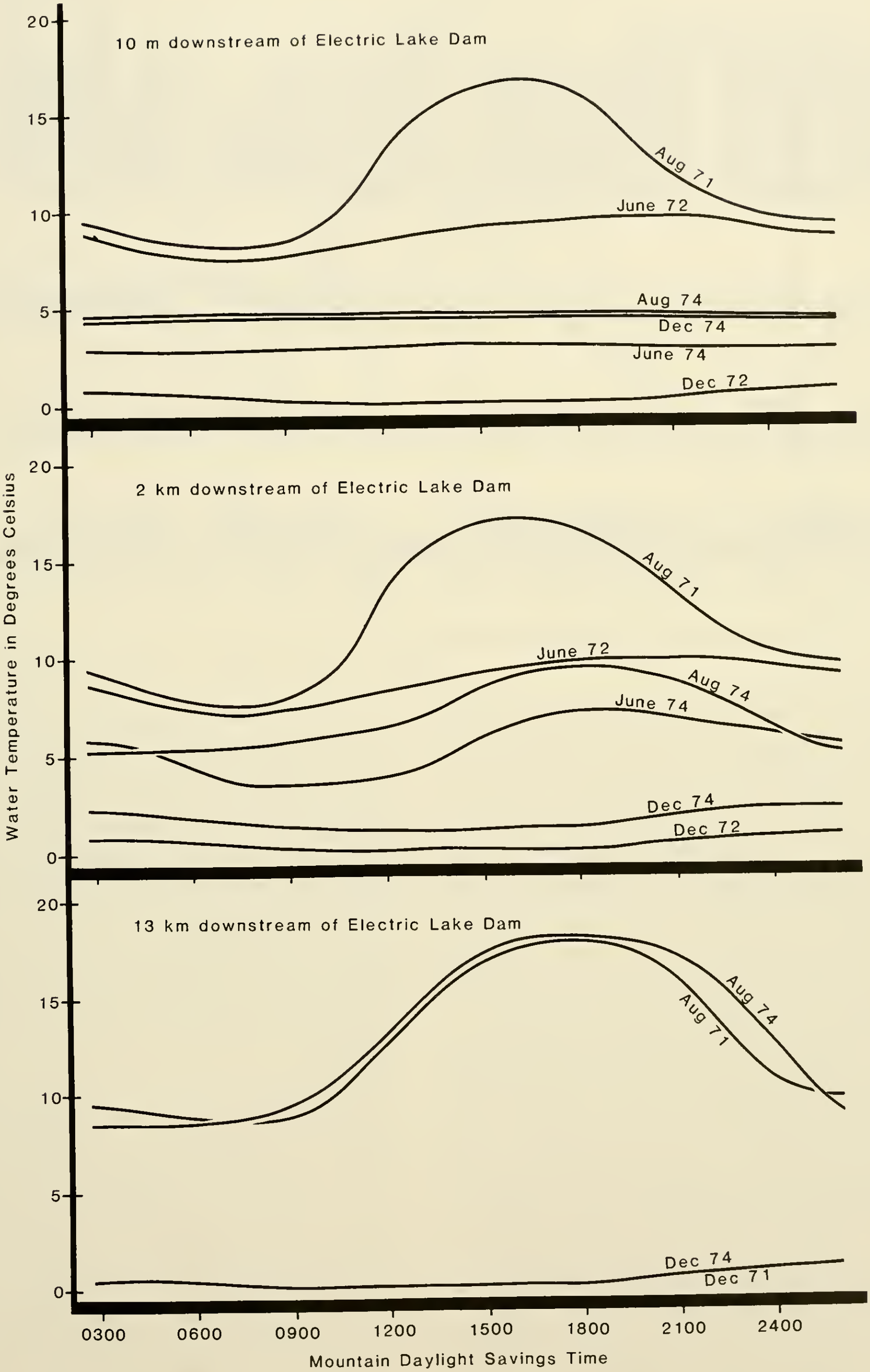

Fig. 5. Fifteen-day mean water temperatures by hour during June, August, and December of 1971 or 1972 (pre-impoundment) and 1974 (early impoundment) at 10 m (outfall), 2 km (Station D-4), and 13 km (Station 7-HSS) downstream from Electric Lake Dam.

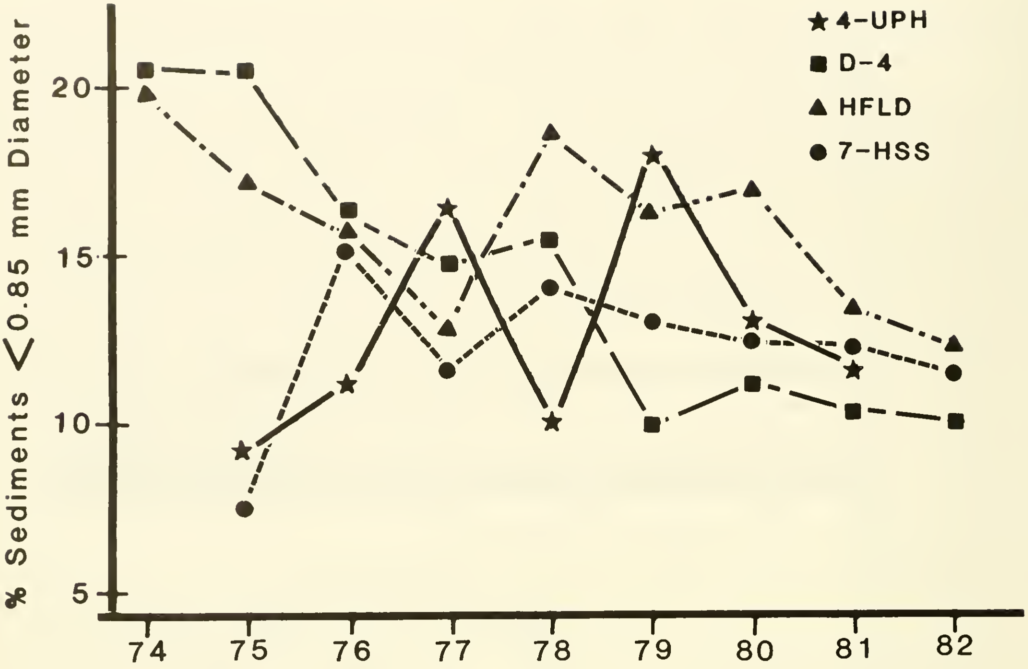

Fig. 6. Annual average percent by weight of sediments with diameter <0.85 mm at four stations on Huntington River 1974–82.

Before Electric Lake, Huntington River spawning gravel beds were composed of 75–90 % gravel, 7–12 % coarse sand, 2–7 % medium sand, and 6–15 % fine sand plus silt/clay. This compares closely to values reported for several California streams (Burns 1970) and the South Fork of the Salmon River (Platts and Megahan 1975). During construction and up through 1982, composition changed below Electric Lake to: 60–85 % gravel, 5–12 % coarse sand, 2–15 % medium sand, and 5–25 % fine sand plus silt/clay.

As in other studies (Cordone and Kelly 1961, McNeil and Ahnell 1964, Burns, 1970), sediment composition of spawning gravels was summarized as percent of the total sample passing through a 0.850-mm mesh screen (Fig. 6). It is assumed that, prior to construction of Electric Lake Dam, percent fines (<0.85mm) at all sampling stations was below 15. McNeil (1964) reported 15 % as the maximum acceptable level of fines for succesful trout spawning. Station 4-UPH, located upstream from reservoir construction activities, was to have been the control station, but construction and other land-use activities upstream resulted in increased loading of fine sediment from 1975 to 1977 (Fig. 6). The moderately low water year of 1976 and the drought of 1977 resulted in a decrease in percent gravels as medium and fine sand plus clay/silt accumulated (Fig. 7). The high water year of 1978 resulted in increased relative gravel content to 1975 levels. The low water year of 1979, in addition to upstream sedimentation, resulted in increased levels of fines. As construction activities ended upstream and stream banks became revegetated, levels of fines dropped from 1980 to 1982.

Following completion of Electric Lake Dam, reservoir gates were closed during the greater part of January and February 1974, reducing flows to 1 cfs (0.03 cms) and less below the reservoir, resulting in a covering of stream substrates with fine clay and silt particles. During periods of natural flows, these materials would have been kept in suspension or deposited in areas of low water velocity. Because of low flows and associated low water energy, even riffle areas were covered and interstitial spaces sealed with fines. Brown trout eggs, alevins, and fry were eliminated from a 10-km reach of stream immedi-

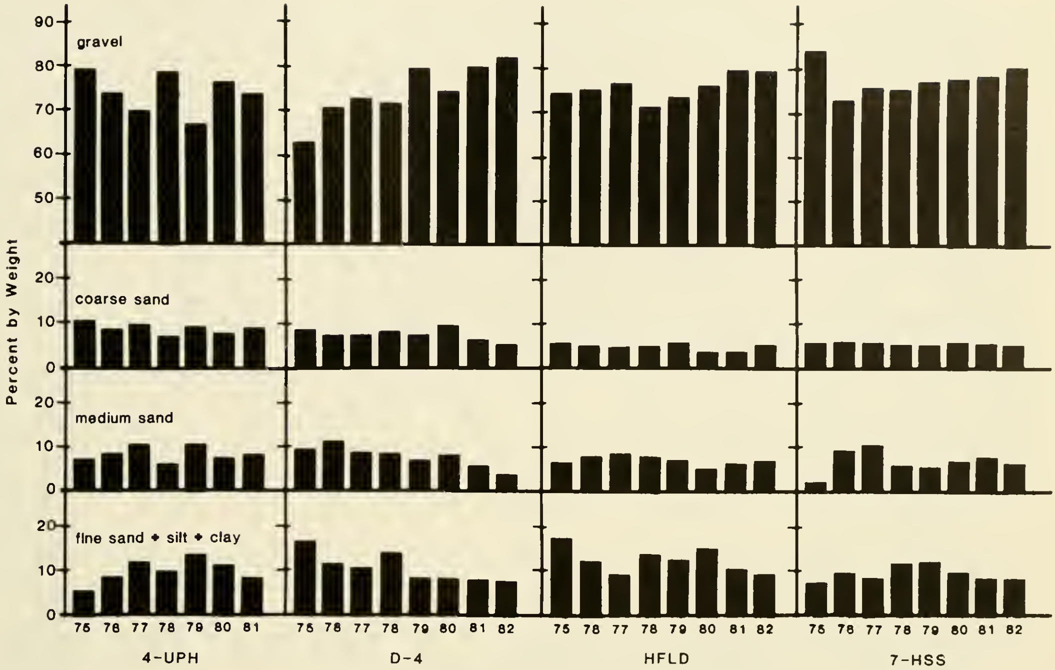

Fig. 7. Annual average by weight sediment composition as gravel, coarse sand, medium sand, and fine sand plus silt and clay for four stations on Huntington River 1975–82.

ately downstream from the dam (pers. comm with John Livesay, UDWR, Price Office; and Gervais 1975). Stoneflies (Plecoptera), mayflies (Ephemeroptera), and caddisflies (Trichoptera) were also largely eliminated from this same stream reach.

Knopp (1978) and Gervais (1975), both employed by the Manti-LaSal National Forest, reported (unpubl. management reports) sediment buildup in Huntington River, largely confined to an 8 km reach of channel immediately below Electric Lake Dam. They concluded that "a reduction in the reproductive potential [for fish] of the channel gravels" had occurred due to the accumulation of "large quantities of sediments over a prolonged period in Huntington River."

During an August 1978 flush, flows were increased from 15–20 cfs (0.4–0.6 cms) to 40–45 cfs (1.1–1.3 cms) and held there 2–3 hr; then increased to 155 cfs (4.4 cms) over a 16-hr period and held 3–4 hr; then flows were increased to 185 cfs (5.2 cms) and held 28–30 hr; then decreased back to 15–20 cfs (0.4–0.6 cms) over a 24-hr period. A total of 4 days were involved. Suspended solids showed a major increase (as mg/l) in immediate response to the first two flow increases, but then levels dropped off rapidly even though flows continued to increase. The flush resulted in a visible decrease in surface fines at Station D-4; but yearly average level of fines increased over 1977 (Fig. 6). At Stations H-FLD and 7-HSS, even though large amounts of fine sediments were put in suspension, considerable amounts remained in the channel. The flush was not of adequate duration or magnitude to transport the large load more than 3–6 km downstream. Thus, even though existing fines were removed from Stations HFLD and 7-HSS, fines from upstream reaches were apparently redeposited, resulting in increased levels. Knopp (1978) concluded that the flush was not adequate to physically move exisiting gravels—that would require flows over 300 cfs (8.5 cms).

Hansen (1970) reported that even at low discharges a stream can move some sand-size material, and the amount of sand in the total sediment load varies considerably between rising and falling stream discharges. When particle-size distribution was determined during floods, suspended sediment concentration (less than 0.063 mm) always peaked at or be-

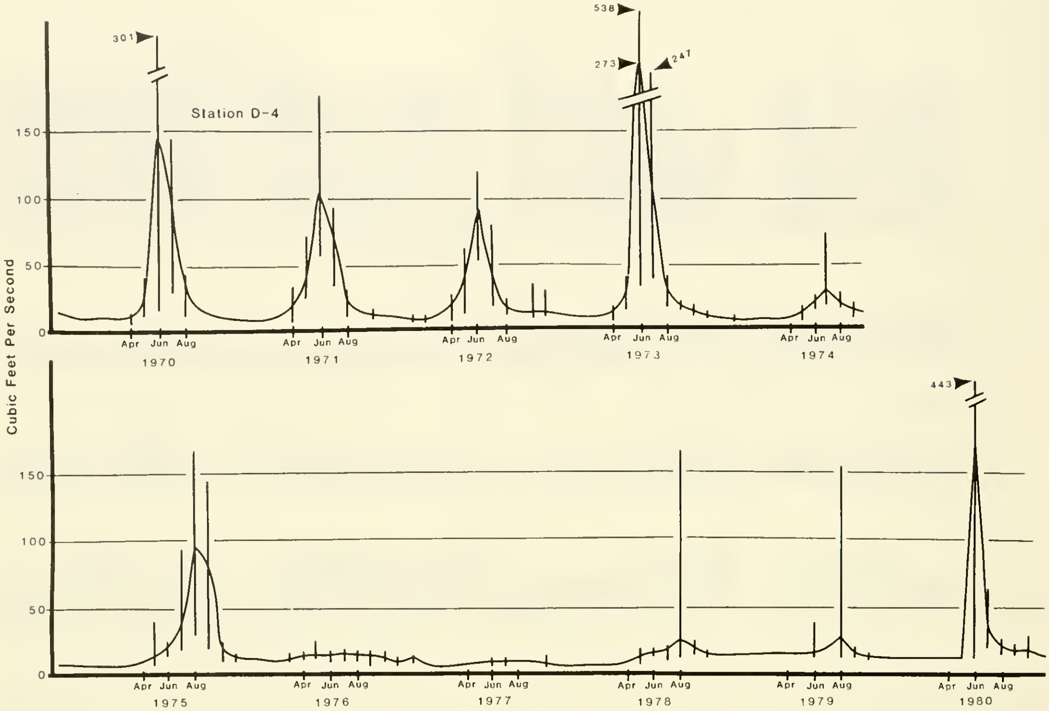

Fig. 8. Monthly average stream flows (cfs), with maximum and minimum daily average flows per month (vertical lines), at Station D-4 (2 km below Electric Lake Dam) for the period 1970–80.

fore the flood peak. However, material greater than 0.062 mm peaked later and displayed an increasing lag as it moved downstream. This lag was apparently due to the natural tendency of coarse bedload material to move at a slower mean velocity than the average stream velocity. The lag may also be related to an increase in channel sediment storage during high flow.

Station D-4, 2 km downstream from Electric Lake Dam, received a heavy load of fines during construction and early reservoir filling (1972–75), but levels of fines decreased each year, 1976 through 1979, and remained low through 1982 (Fig. 6). Reduction in fines was due to a loss of silt, clay and fine and medium sand, with a corresponding increase in gravels (Fig. 7).

At Station HFLD, levels of fines decreased yearly, from 1975 through 1977 (Fig. 6). In 1978 a large load of fines, mainly fine sand, silt, and clay (Fig. 7), was deposited at Station HFLD, probably the result of the August flush bringing accumulated fines from upstream areas. Levels of fines decreased from 1978 through 1982, but still remained higher than at the other stations.

Sediments at Station 7-HSS showed no impacts from upstream construction until 1976 — levels of fines during 1975 averaged only 8 % (Fig. 6) with gravels accounting for 86 % of the total (Fig. 7). Levels of fines nearly doubled in 1976 (15 %) and gravels dropped to only 75 %. The August 1978 flush resulted in a reduction in medium sands and an increase in silt, medium, and fine sand. From 1978 to 1982 the trend, although weak, was an increase in gravels and a decrease in fine sands, silts, and clays.

Stream Discharge

Prior to 1974, stream flows in Huntington River above Left Fork were similar to most natural mountain streams — low, nearly constant flows at 4–25 cfs (0.1–0.7 cms) from August through March; a rapid increase during spring snow-melt occurring somewhere from April through June, with monthly means between 75–200 cfs (2.1–5.7 cms); and a gradual decline through June and July (Fig. 8).

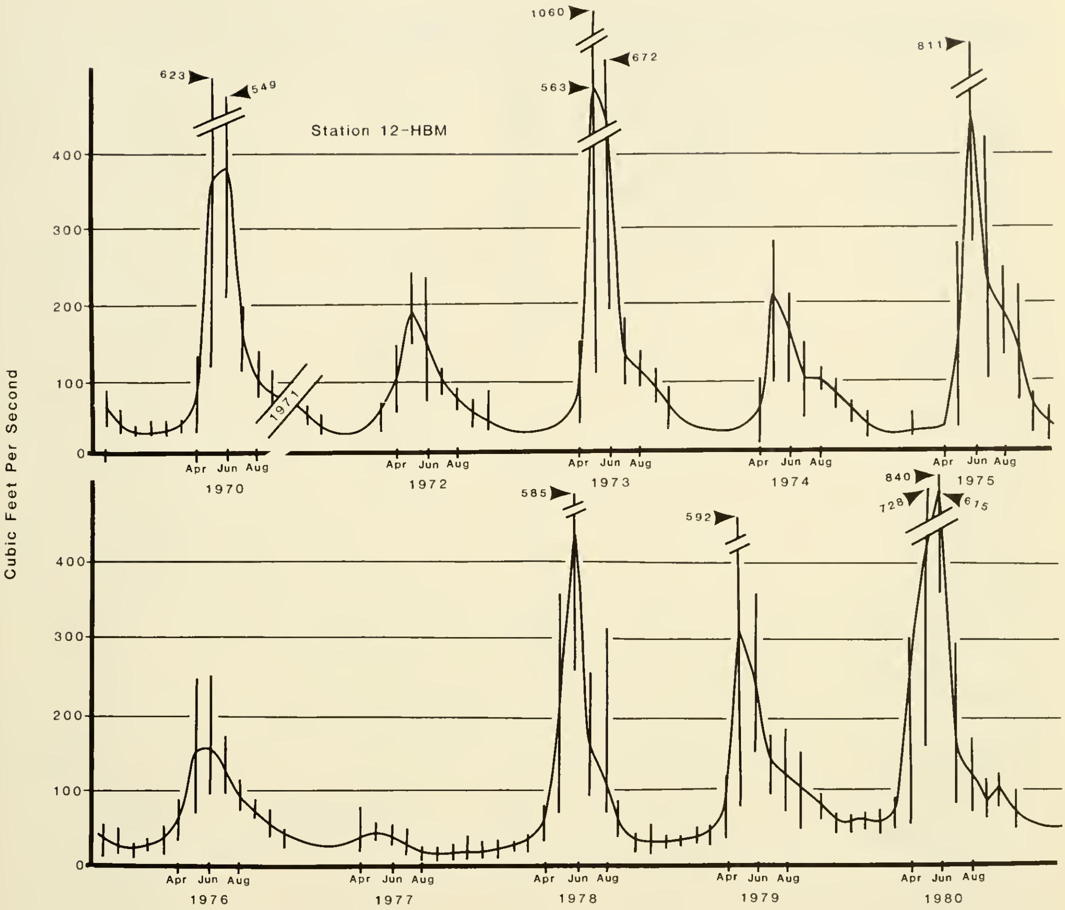

Fig. 9. Monthly average stream flows (cfs), with maximum and minimum daily average flows per month (vertical lines), at Station 12-HBM (32 km below Electric Lake Dam) for the period 1970–80.

Following completion of Electric Lake Dam (fall of 1973), flows above the dam continued to reflect the natural hydrological cycle of the canyon, including low flows during 1976 and the 1977 drought. Below the dam flows were regulated. A drawdown of the reservoir in 1975 resulted in high flows from July through September, rather than from April through June. Flushing flows were released in August 1978 and 1979, with flows of 150–190 cfs (4.2–5.4 cms) and 160 cfs (4.5 cms) for 3 days each, respectively. In 1980, spring runoff filled Electric Lake completely and water spilled over the top of the spillway for the first time, resulting in flows over 400 cfs (11.3cms) during the month of June.

Left Fork Huntington Creek doubles the flow of Huntington River, on the average, plus several other small tributaries enter the river above Station 12-HBM. Below Left Fork, stream flows reflected a near natural flow pattern, with the exception that increases were more gradual in the spring and peak flows were extended into June and July (Fig. 9). This was the result of prerunoff and summer irrigation releases from upstream Left Fork reservoirs.

Macroinvertebrate Communities

The macroinvertebrate community of Huntington River is diverse, containing representatives inhabiting all major stream habitats, exhibiting all general stream organism habits, and exploiting all available energy types (Table 1). There are taxa considered intolerant (TQs < 36) to environmental changes as well as those classified as extremely tolerant (TQs > 90). The high quality of

TABLE 1. List of taxa collected within the Huntington River system, with habitat[a], habit[b], trophic relationships[c] and tolerance quotients for selected taxa, plus the percent frequency in which each was collected in quantitative samples. Habitat, habit and trophic relationships were largely taken from Merritt and Cummins (1978).

	Habitat	Habit	Trophic	TQ	Frequency
Nematoda	1,2	1,2,5	1,det	108	80.6
Gastropoda	1,2	1,2,3	1,2,3,5	108	5.0
Lymnaeidae					
Lymnaea	1,2	1,2,3	1,2,3,5	108	8.8
Physidae					
Physa	1,2	1,2,3	1,2,3,5	108	10.6
Planorbidae				108	10.6
Pelecypoda	1,2	1,5	4	108	35.0
Clitellata					
Oligochaeta	2	2,5	1,2	108	98.8
Hirudinea	1	1	6,8	108	2.5
Turbellaria				108	11.9
Planaria	2	2	1,2,3	108	0.6
Tardigrada					
Hydracarina	1,2	1	7,8	108	87.5
Crustacea					
Amphipoda	1,2	3,4	1,2		13.1
Gammaridae				108	0.6
Cladocera				108	2.5
Daphnia	2	3,4	1,3,4		18.7
Copepoda	2	3,4	1,3,4,det,inv	108	50.0
Cyclops					
Diaptomis					
Ostracoda	1,2	3,5	1,2,4	108	53.8
Insecta					
Ephemeroptera					
Siphlonuridae				72	0.6
Ameletus	1,2	3,4	1,2,det,dia	72	4.4
Siphlonurus occidentalis	1,2	3,4	1,2,3,6,inv,det	72	
Baetidae					
Baetis	1,2	1,3,4	1,2,3,det,dia	72	93.1
tricaudatus					
alexanderi					
bicaudatus					
intermedius					
parvus					
Callibaetis coloradensis	2	2,4	1,2,3,det	72	
Heptageniidae				48	4.4
Heptagenia	1	1,4	1,2,3	54	45.0
Cinygmula	1,2	1	1,2,3,det,dia	30	68.1
Rhithrogena robusta	1	3	1,2,det,dia	21	45.0
Epeorus longimanus	1	1	1,2,3,det,dia	21	28.1
Leptophlebiidae					
Paraleptophlebia heteronea	1,2	1,2,4	1,2,5,det,dia	24	24.4

[a] Habitat
1 = erosional
2 = depositional

[b] Habit
1 = clingers
2 = sprawlers
3 = climbers
4 = swimmers
5 = burrowers
6 = net spinners
7 = tube makers
8 = case makers
9 = divers
10 = skaters

[c] Trophic relationship
1 = collectors
2 = gatherers
3 = scrapers
4 = filterers
5 = shredders
6– engulfers
7 = piercers
8 = parasitic

det = detritus
dia = diatoms
alg = algae
inv = invertebrates
ani = animals

Table 1 continued.

	Habitat	Habit	Trophic	TQ	Frequency
Ephemerellidae				48	2.5
Ephemerella	1,2	1,2,4	1,2,det,dia	48	25.6
grandis	1,2	1,2	1,2,det,dia	24	65.6
doddsi	1	1,2	1,2,3,det,dia	2	15.6
coloradensis	1	1,2	1,2,det,dia	18	8.8
inermis	1,2	1,2	1,2,det,dia	48	73.1
tibialis	1	1,2	1,2,det,dia	24	16.2
Caenidae					
Caenis	2	2	1,2,3,det	72	0.6
simulans					
Tricorythidae					
Tricorythodes	1	1,2	1,2,3,det	108	12.5
minutus					
Odonata					
Libellulidae					
Libellula	2	2	6,inv,ani	72	
quadrimaculata					
Gomphidae					
Erpetogomphus	2	5	6,inv,ani	72	0.6
compositus					
Ophiogomphus	1,2	5	6,inv,ani	108	11.2
severus					
Coenagrionidae				108	0.6
Argia	1,2	1,2,3	6,inv,ani	108	13.1
Agrion	1,2	1,2,3	6,inv,ani	108	
Agrionidae					
Hetaerina	1,2	1,3	6,inv,ani	108	1.2
americana					
Plecoptera					
Nemouridae				24	6.9
Amphinemura	1,2	1,2	1,2,5,det	6	1.2
mogollonica					
Malenka	1,2	1,2	1,2,5,det	36	
californica					
Prostoia	1,2	1,2	3,5,det	24	20.6
besametsa					
Podmosta	1,2	1,2	5,det	12	0.6
delicatula					
Zapada	1	1,2	5,det	16	12.5
cinctipes				16	6.2
haysi					
Nemoura	1,2	1,2	1,2,5,det	24	3.8
Capniidae	1,2	1,2	5,det	32	28.1
Capnia	1,2	1,2	5,det	32	
confusa					
gracilaria					
nana wasatchae					
Eucapnopsis	1,2	1,2	5,det	18	
brevicauda	1,2	1,2	5,det	24	
Isocapnia					
crinita					
vedderensis					
Utacapnia	1,2	1,2	5,det	18	
logana					
Taeniopterygidae					
Taenionema	1,2	1,2	1,2,3,5,det	48	8.1
nigripenne					
Pteronarcyidae					
Pteronarcella	1,2	1,2	3,5,6	24	50.6
badia					
Pteronarcys	1,2	1,2	3,5,6,det	18	20.6
californica					

Table 1 continued.

	Habitat	Habit	Trophic	TQ	Frequency
Perlodidae				48	29.4
Cultus	1	1	6	12	1.2
aestivalis					
Isogenoides	1,2	1	6,inv	24	38.8
zionensis					
Diura	1	1	3,6	24	1.9
knowltoni				24	2.5
Isoperla	1,2	1,2	1,2,6,inv	48	33.1
fulva				48	30.0
ebria				24	0.6
patricia					
petersoni					
quinquepunctata					
Megarcys	1	1	6,3	24	8.8
signata					
Skwala	1	1	6,inv	18	5.0
parallela					
Chloroperlidae	1	1	1,2,3,6,det,inv	24	50.6
Alloperla					
severa					
Sweltsa					
coloradensis					
Suwallia					
pallidula					
Triznaka					
diversa					
signata					
Leuctridae					
Perlomyia	1	1,2	5,det	18	
utahensis					
Perlidae				24	0.6
Hesperoperla	1	1	6,inv,ani	18	9.4
pacifica					
Peltoperlidae					
Yoraperla	1,2	1,2	3,5,det	24	1.2
Hemiptera					
Saldidae	2	3	7,inv,ani	90	0.6
Notonectidae					
Notonecta	1,2	4	7,inv,ani	108	
Corixidae	1,2	4	7,6,alg,inv,det	108	
Gerridae					
Gerris	1,2	10	7,inv,det	72	
Mesoveliidae					
Mesovelia	1,2	10,2,3	7	108	
Veliidae					
Rhagovelia	1	10	7,inv	104	
Megaloptera					
Sialidae					
Sialis	1,2	1,3,5	inv,ani	72	1.2
Trichoptera					
Rhyacophilidae					
Rhyacophila	1	1	1,2,3,5,6	18	56.9
coloradensis					
Hydropsychidae					6.2
Hydropsyche	1	1,6	1,4,det,inv	108	67.5
Arctopsyche	1	1,6	1,4,det,inv	18	41.2
grandis					
inermis					
Cheumatopsyche	1	1,6	1,4,det,inv	108	2.5

Table 1 continued.

	Habitat	Habit	Trophic	TQ	Frequency
Psychomyiidae					
Psychomyia flavida	1,2	1,6	1,2,det,inv	108	
Hydroptilidae				108	3.8
Hydroptila	1,2	1,8	3,7,det,alg	108	14.4
Ochrotrichia	1,2	1,8	1,2,7,alg,dia	108	3.8
Stactobiella	1,2	1,8		108	0.6
Limnephilidae					7.5
Asynarchus nigriculis	1,2	1,2,3,8	1,2	108	
Limnephilus castor	1,2	1,2,3,8	1,2,5,det	108	1.2
Dicosmoecus atripes	1	2	3	24	5.6
Hesperophylax consimilis	1,2	2	5,det	108	6.2
Oligophlebodes minutus	1	1	1,2,3	24	24.4
Grammotaulius loerttae	1,2	3	1,2,3	108	0.6
Neothremma	1	1	1,2,3	8	1.9
Onocosmoecus	2	2	5	18	0.6
Leptoceridae					
Oecetis	1,2	1,2,3	5,6	54	1.2
Lepidostomatidae					
Lepidostoma	1,2	1,2,3	5,det	18	11.9
Brachycentridae					
Brachycentrus americanus occidentalis	1	1,8	1,4,3,det,dia	24	63.1
Micrasema	1	2,8	1,2,5,det	24	8.1
Oligoplectrum	1	1	1,2,3,det,dia	24	0.6
Glossosomatidae					
Glossosoma	1	1	1,2,3,det,alg	24	0.6
Protoptila	1	1	1,2,3,dia,det	32	1.2
Philopotamidae					
Chimmara	1	1	1,4	24	0.6
Lepidoptera					
Pyralidae					
Paragyractus kearfottalis	2	3,4,5	5	72	1.9
Coleoptera					1.2
Haliplidae					
Halipus	1	3	5,7,alg	54	3.1
Brychius	1,2	1	3,7,alg	54	
Dytiscidae	2	3,4	6,7,inv,ani	72	4.4
Deronectus dolerosus	1,2	3,4	7,inv,ani	72	
Agabus	1,2	4,9	7,inv,ani	72	
Acilius semiguleatus	1,2	4,9	7,inv,ani	72	
Oreodytes	1,2	3,4	7,inv,ani	72	
Rhantus	1,2	4,9	7,inv,ani	72	
Hydrophilidae	2	3	1,2,6,7	72	2.5
Helophorus	1,2	3	7,det	72	
Crenitis	1,2	5		72	
Ametor	1,2	1	1,2	72	
Elmidae	1,2	1,3	1,2,3,det,dia	104	84.4
Cleptelmis					
Heterlimnius					
Narpus					
Optioservus					

Table 1 continued.

	Habitat	Habit	Trophic	TQ	Frequency
Hydraenidae					
Hydraena	1	3,4	6,inv,ani	72	
Dryopidae					
Helichus	1,2	3	5,det	72	5.6
Amphizoidae					
Amphizoa	1,2	1	6,inv	24	
Diptera					
Tipulidae				108	1.9
Antocha	1	1	1,2	72	24.4
monticola					
Dicranota	1,2	2,5	1,5,6,inv,det	24	51.2
Tipula	1,2	5(det)	1,2,3,5,6	72	2.5
G (formerly called					
Holorusia grandis)				72	24.4
Eriocera	1,2	1,2,5	5,6,det,inv	72	48.1
Limnophila	1,2	5	6,inv	72	
Pseudolimnophila	1,2	5	6,inv	72	
Psychodidae					
Pericoma	2	5	1,2	36	16.9
Deuterophlebiidae					
Deuterophlebia	1	1	3	4	1.9
coloradensis					
Culicidae					
Aedes	2	4	1,4	108	3.1
hexodontus					
Chaoboridae					
Chaoborus	2	2,4	6,7,inv	104	
Dixidae	1	3,4	1,2	108	2.5
Dixa					
Simuliidae	1	1	1,4,det,alg	108	93.1
Simulium					
articum					
aureum					
canadense					
vittatum					
Prosimulium					
onychodactylum					
Cnephia					
Chironomidae	1,2	2,5,7	1,2,4,6,7	108	100.0
Ceratopogonidae	2	2,5	1,2,6,inv,det	108	41.2
Culicoides	2	1,2	1,2,6,det,inv	108	
Forcipomyia	1,2	1,2	1,2,3,det,alg	90	
Stratiomyidae					
Euparyphus	1	2	1,2,3	108	8.1
Tabanidae	2	2,5	7,inv,ani	108	2.5
Chrysops	2	2,5	1,2	100	
Tabanus	2	2,5	7	108	
Rhagionidae					
Atherix	1,2	2,5	7	24	50.6
pachypus					
Dolichopodidae	2	2,5	6	108	1.2
Empididae					
Hemerodromia	1,2	2,5	1,2,6,inv,ani	95	80.0
Muscidae					
Limnophora	1	5	6,inv	108	10.0
Ptychopteridae	2	5	1,2	48	2.5
Ptychoptera					
Tanyderidae	1	2	5	72	2.5
Ephydridae	1,2	2,4	1,2,5	108	

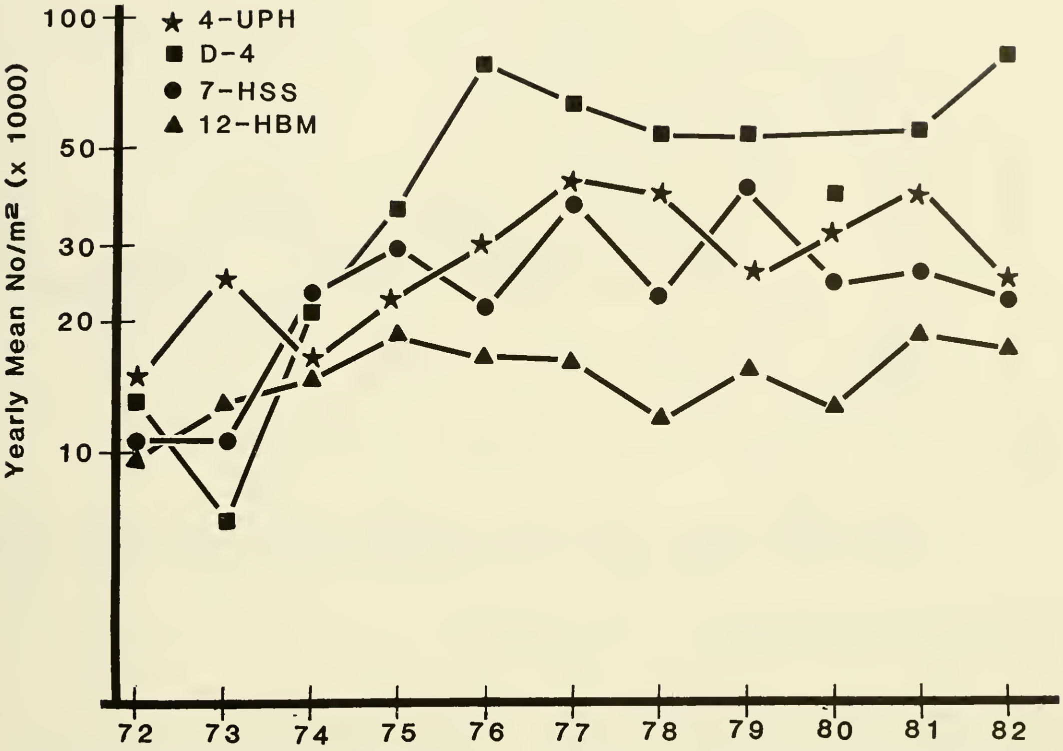

Fig. 10. Yearly average number of macroinvertebrates per square meter per sampling date at four stations on Huntington River for the period 1972–82.

Huntington River is attested to by the high percent frequency in quantitative samples of taxa with low TQ values.

At Station 4-UPH, from 1976 to 1977, a trend developed of increasing numbers but decreasing weight (Figs .10 and 11). This reflects a reduction in averge size per individual (Fig. 12) — numbers of larger-sized individuals decreased in relation to numbers of smaller individuals. Stress often has this effect on aquatic macroinvertebrate communities. Construction upstream during the 1973–77 period added sediment and organic enrichment to the upper section of Huntington River. The drainage was also receiving heavy recreational and grazing use, adding additional organic enrichment and sedimentation. The moderate water year of 1976 and the 1977 drought amplified the impacts of these environmental stresses. Conditions began to improve in 1978, as shown by an increase in dry weight associated with a decrease in numbers. Numbers in 1981, a low water year, had increased to 1977 levels, but dry weight was more than double that of 1977. High biomass continued through 1982, showing a marked improvement in the community.

Numbers and weights at Station D-4 were nearly the same as those at Station 4-UPH during 1972, even though highway bridge construction was in progress 0.8 km upstream. In June 1973 a spring flood washed out footings of the bridge, adding sands and silts that scoured the substrates at Station D-4 and eliminated most macroinvertebrates. In January 1974 reservoir release gates were almost closed, with flows less than 1 cfs (0.03 cms) for several days, eliminating most invertebrate taxa from this station. During the summer of 1974 numbers increased dramatically (Fig. 10), but with only a slight increase in weight (Fig. 11). In 1975, 1976, and 1977 the difference between numbers and weights continued to increase yearly, as shown by decreasing mean weight per individual (Fig. 12). Benthic communities below reservoirs have been noted to dramatically increase in numbers, with an increase in relative number of small larvae, following completion of dam construction (Williams and Winget 1979).

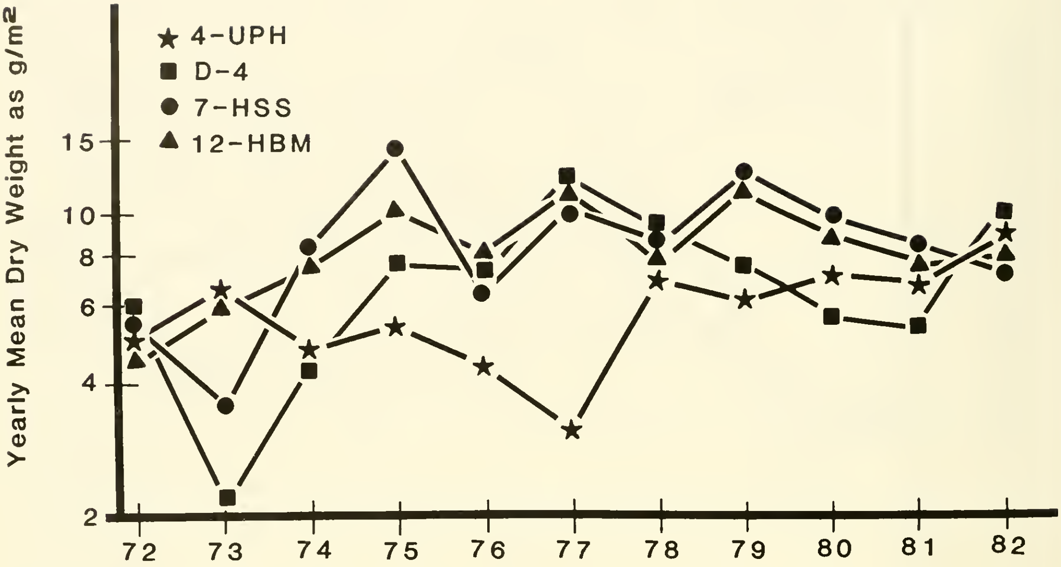

Fig. 11. Yearly average dry weight of macroinvertebrates per square meter per sampling date for four stations on Huntington River for the period 1972–82.

From 1977 to 1981, annual mean weight continued to decrease each year while numbers remained high. During 1982 there was an increase in both numbers and weight, but mean weight per organism remained low.

At Station 7-HSS the macroinvertebrate community showed an increase in numbers from 1973 to 1977 (Fig. 10), but not as dramatic as at Station D-4. From 1977 to 1982 numbers seemed to oscillate around a rather stable mean. Biomass was higher from 1974 to 1982 than in 1972 or 1973 (Fig. 11). At Station D-4 large larvae were largely eliminated and replaced by species with smaller larvae, but at Station 7-HSS it appears that reduction in large larvae was insignificant (Fig. 12). This represents a reduced impact on the aquatic community at Station 7-HSS compared to Station D-4.

The macroinvertebrate community at Station 12-HBM showed a slight increase in annual mean numbers from 1972 to 1975, a decreasing density trend from 1975 to 1978, and then an oscillation around a stable mean slightly higher than preimpoundment numbers (Fig. 10). Biomass increased from 1972 to 1975 and then seemed to stabilize at an increased level from 1975 through 1982 (Fig. 11). Mean size of community members, as average weight per organism, remained high through 1972 to 1982, with a high in 1979 and a low in 1981 (Fig. 12).

Stations 4-UPH, 7-HSS, and 12-HBM had approximately the same number of taxa per sample date (Table 2). Numbers of taxa were lower at Station D-4 but increased each year from 1978 to 1981, with a drop again in 1982.

Community Tolerance Quotients (CTQa) were similar at Stations 4-UPH, 7-HSS, and 12-HBM, indicating similar relative environmental tolerances of community members (Table 2). CTQa values were slightly lower at Stations 7-HSS and 12-HBM than at 4-UPH, a natural occurrence in a high quality stream — community diversity and quality increasing downstream until water quality or habitat deterioration begins, usually near the mouth of the canyon. Then the opposite occurs. Station D-4 had CTQa values considerably higher than the other stations, but note the yearly decrease from 1978 to 1981, a definite improvement trend below the dam. Biotic Condition Index (BCI) values showed a yearly improvement at Station D-4 and also illustrated the stresses of organic enrichment and sedimentation above Electric Lake at Station 4-UPH, showing the poorest condition during the low water year of 1981.

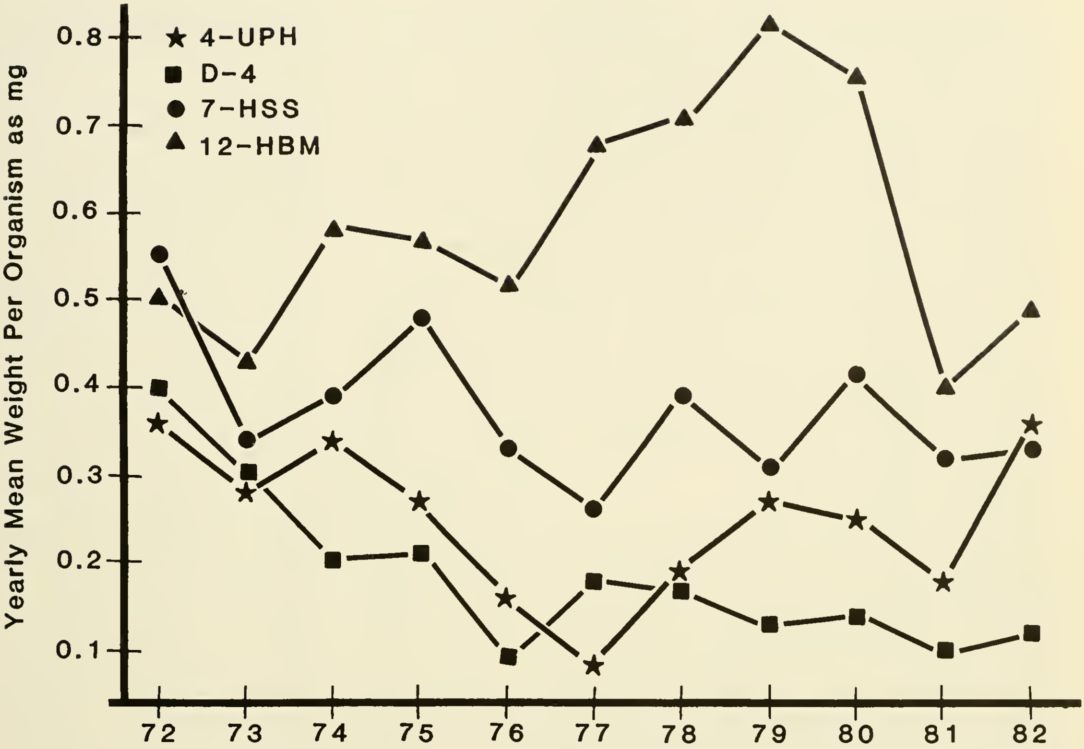

Fig. 12. Yearly average weight per macroinvertebrate (average yearly total dry weight divided by average yearly total number) at four stations on Huntington River for the period 1972–82.

Station 4-UPH had only slight dominance by tolerant taxa during all five years, as shown by the small difference between CTQa and CTQd (Table 2). Station 7-HSS had moderate community dominance by tolerant taxa during 1978, 1979, and, 1980 but a noticeable improvement occurred by 1981 and continued through 1982. Station 12-HBM macroinvertebrate community had a higher proportion of environmentally fragile taxa than Station 4-UPH (lower CTQa), but they were dominated number-wise by more environmentally tolerant species (CTQa–CTQd was greater). The community at Station 12-HBM represents a transition between the high canyon community and the lower canyon or valley communities. At Station D-4, CTQa–CTQd had a large difference (-5.5 average for all five years), indicating an unstable community structure under strong influence toward a more environmentally tolerant species composition.

The average H (Shannon-Weaver) dominance diversity index value of 1.90 at Station D-4 indicated a community dominated number-wise by a few species (Table 2), and the CTQd values show these dominant species were environmentally tolerant. Dominance diversity (H) and CTQd values indicated that Stations 7-HSS and 12-HBM were intermediate in community condition to Stations 4-UPH and D-4, illustrating moderate impact from Electric Lake compared with Station D-4. All three stations below Electric Lake showed a general recovery trend from 1978 through 1981.

Cinygmula, usually found on the surface of stable subtrates such as rubble or larger sized rocks, require at least some substrates clean of fine sediments or excessive algal growth. Species of *Cinygmula* are among the more sediment-tolerant of the family Heptageniidae. *Cinygmula* nymphs in Huntington River hatch from eggs in late fall to early winter, develop during the winter and spring, and emerge as adults in late spring through early summer following peak spring runoff. Eggs hatch approximately one month after being laid. *Cinygmula* were either in the adult or egg stages during August flushes.

At Station 4-UPH, numbers of *Cinygmula* dipped slightly from 1975 though 1977 as silt and organic enrichment entered the stream from construction and recreation upstream (Table 3). From 1978 to 1982, numbers of *Cinygmula* increased as land-use impacts decreased and increased runoff cleaned substrates of fine sediments. Below Electric Lake at Station D-4, numbers dropped during construction of Electric Lake Dam and remained low through 1978. Flushing of accumulated fine sediments from the substrates from 1975 to 1979 resulted in increasing numbers from 1978 through 1981. Numbers also increased at Stations 7-HSS and 12-HBM, probably due to moderated flows, decreased turbidity, and increased diatom growths.

The mayfly *Rhithrogena robusta* looks much like the mayfly *Cinygmula*, but gills of *Cinygmula* project dorso-laterally from the abdomen and gills of *R. robusta* extend from the ventral surface of the abdomen and overlap in such a as way to appear and function almost like a suction cup pressed against the rock. This aids *Rhithrogena* in maintaining position on rock surfaces in swift currents found in areas of clean, smooth, and angular substrates (Gore 1978), common to Huntington River. Gore (1977) reported that high water releases from a reservoir (over 120 cfs in his study) caused *Rhithrogena* to drift downstream. *Rhithrogena robusta* were present either as emerging adults or early instar larvae during August flushes, making it vulnerable to sediment movements and increased velocities associated with these flushes.

At Stations 7-HSS and 12-HBM, *R. robusta* increased in numbers from 1972 through 1982 (Table 3). At Station D-4, *R. robusta* were present before impoundment (1972), but were not found from 1973 through 1980. A few were collected in 1981 but were absent again in 1982. According to Humpesch and Elliot (1980), many species of *Rhithrogena* have temperature requirements for egg hatch. It is possible that at Station D-4 water temperatures may not have provided the proper stimulus. But, since Station D-4 is almost 2 km below the dam and water temperatures had responsed noticeabley to physical environment at this point (Fig. 5), it is probable that increases in siltation and algal growth plus regulated flows were responsible for eliminating *R. robusta*.

Table 2. Summary of aquatic macroinvertebrate community conditions at stations 4-UPH, D-4, 7-HSS, and 12-HBM from 1978 through 1982.

	4-UPH	D-4	7-HSS	12-HBM	4-UPH	D-4	7-HSS	12-HBM
	Number of taxa				H (Shannon-Weaver)			
1978	29.8	19.4	27.0	26.0	2.63	1.93	2.52	2.81
1979	33.3	22.6	30.4	29.8	2.94	1.78	2.53	3.12
1980	24.0	22.6	28.0	29.2	2.85	2.08	3.02	3.13
1981	30.0	28.5	32.7	32.2	3.27	2.20	3.45	3.23
1982	35.0	23.2	31.8	31.8	3.70	1.50	3.27	2.96
MEAN	30.4	23.3	30.0	29.8	3.08	1.90	2.96	3.05
	CTQa				CTQd			
1978	62.0	80.8	60.3	58.8	63.0	87.8	63.9	65.3
1979	56.7	67.4	56.6	58.0	59.3	74.2	61.4	62.2
1980	61.7	66.0	59.0	56.3	63.7	72.6	62.3	60.5
1981	65.5	64.5	57.0	60.7	64.5	68.2	56.8	64.5
1982	60.0	67.6	59.4	59.8	62.0	71.4	59.0	64.4
MEAN	61.2	69.3	58.5	58.7	62.5	74.8	60.7	63.4
	BCI				CTQa minus CTQd			
1978	88.6	68.0	92.0	95.3	-1.0	-7.0	-3.6	-6.5
1979	97.0	81.0	98.4	95.7	-2.6	-6.8	-4.8	-4.2
1980	89.3	83.6	94.0	98.5	-2.0	-6.6	-3.3	-4.2
1981	84.0	85.3	96.5	90.7	1.0	-3.7	0.2	-3.8
1982	91.7	81.4	92.6	92.0	-2.0	-3.8	0.4	-4.6
MEAN	90.1	79.9	94.7	94.4	-1.3	-5.5	-2.2	-4.7

TABLE 3. Mean number per square meter and standard error of mean (in parentheses) for several taxa at four stations on Huntington River, Utah.

Year	4-UPH	D-4	7-HSS	12-HBM	4-UPH	D-4	7-HSS	12-HBM
	Cinygmula				*Rhithrogena robusta*			
1972	1493	222	111	150	0	42	39	159
	(1355)	(62)	(13)	(96)		(20)	(12)	(51)
1973	2930	62	53	133	0	0	8	96
	(2061)	(39)	(18)	(49)			(4)	(32)
1974	3438	29	102	434	0	0	45	206
	(2039)	(11)	(45)	(178)			(13)	(56)
1975	542	42	302	1292	0	0	40	168
	(139)	(10)	(69)	(149)			(13)	(51)
1976	1108	21	78	348	0	0	220	168
	(407)	(21)	(37)	(332)			(136)	(101)
1977	1238	40	370	1324	0	0	319	453
	(1237)	(31)	(218)	(698)			(131)	(168)
1978	3728	42	202	383	0	0	32	233
	(1601)	(17)	(56)	(209)			(8)	(92)
1979	1697	131	666	384	0	0	100	304
	(576)	(37)	(280)	(216)			(70)	(282)
1980	1965	492	944	1266	0	0	53	208
	(641)	(415)	(440)	(903)			(23)	(78)
1981	4939	963	2322	1712	0	11	212	149
	(75)	(355)	(578)	(840)		(7)	(156)	(63)
1982	2066	234	1181	161	0	0	196	137
	-	(96)	(226)	(56)			(89)	(86)
	Ephemerella grandis				*Ephemerella doddsi*			
1972	32	474	458	36	209	107	1	0
	(12)	(145)	(107)	(7)	(126)	(56)	(1)	
1973	333	347	350	115	683	133	2	0
	(208)	(68)	(149)	(37)	(285)	(46)	(1)	
1974	19	1482	282	27	232	4	3	0
	(13)	(322)	(35)	(5)	(53)	(2)	(2)	
1975	4	591	317	17	359	0	0	0
	(4)	(257)	(49)	(3)	(359)			
1976	36	270	593	46	174	0	1	0
	(6)	(158)	(175)	(34)	(83)		(1)	
1977	40	1082	732	22	15	0	0	0
	(25)	(744)	(62)	(12)	(14)			
1978	53	142	236	38	108	0	0	0
	(22)	(63)	(46)	(18)	(42)			
1979	11	74	279	86	60	0	0	0
	(11)	(45)	(127)	(33)	(45)			
1980	0	7	266	57	131	3	4	0
		(7)	(85)	(26)	(72)	(3)	(4)	
1981	0	388	834	69	302	0	9	0
		(244)	(518)	(30)	(236)		(9)	
1982	43	152	582	71	560	9	6	0
	-	(60)	(234)	(28)	-	(6)	(4)	
	Pteronarcella badia				*Brachycentrus*			
1972	0	15	181	227	0	98	445	39
		(6)	(20)	(39)		(46)	(197)	(23)
1973	0	14	117	222	0	38	328	37
		(7)	(40)	(37)		(10)	(99)	(9)
1974	0	37	465	519	0	7	1023	44
		(11)	(72)	(107)		(2)	(219)	(8)
1975	0	20	464	473	0	5	566	127
		(9)	(33)	(56)		(2)	(133)	(30)
1976	0	2	158	526	0	0	180	14
		(2)	(64)	(141)			(55)	(7)

Table 3 continued.

Year	4-UPH	D-4	7-HSS	12-HBM	4-UPH	D-4	7-HSS	12-HBM
	Pteronarcella badia				*Brachycentrus*			
1977	0	22	112	193	0	164	639	48
		(15)	(46)	(46)		(164)	(238)	(30)
1978	0	0	80	230	0	186	701	80
			(26)	(113)		(81)	(193)	(17)
1979	0	0	58	304	0	54	1475	138
			(26)	(48)		(46)	(528)	(85)
1980	0	1	25	259	0	90	491	138
		(1)	(21)	(118)		(58)	(104)	(52)
1981	0	0	257	237	0	135	841	82
			(90)	(67)		(57)	(244)	(29)
1982	0	1	41	129	0	48	274	29
		(1)	(18)	(53)		(28)	(81)	(10)
	Arctopsyche grandis				*Chironomidae*			
1972	0	45	127	109	4382	3173	1434	1653
		(19)	(23)	(36)	(1296)	(458)	(260)	(491)
1973	0	103	145	169	4712	2307	2059	1764
		(55)	(65)	(66)	(1503)	(739)	(291)	(341)
1974	0	27	122	37	1759	15745	7355	2092
		(9)	(39)	(8)	(712)	(2798)	(1049)	(350)
1975	0	22	119	33	5181	21420	12390	2501
		(11)	(8)	(10)	(2055)	(4402)	(3494)	(322)
1976	0	4	167	234	10310	58107	5740	4162
		(4)	(96)	(140)	(1114)	(27716)	(2535)	(2424)
1977	0	92	125	76	21594	26782	14031	1154
		(92)	(57)	(23)	(4521)	(2464)	(6004)	(278)
1978	0	40	44	35	11914	26007	8844	2067
		(34)	(13)	(8)	(1321)	(5676)	(1872)	(454)
1979	0	23	29	80	5472	37200	8229	2057
		(16)	(9)	(50)	(2375)	(16389)	(2529)	(719)
1980	0	24	168	73	5832	11760	5475	1959
		(20)	(74)	(35)	(1857)	(4810)	(1655)	(542)
1981	0	24	255	124	8092	18608	4369	1936
		(11)	(88)	(75)	(2087)	(3432)	(808)	(366)
1982	0	14	144	107	3658	44475	2849	1467
		(9)	(59)	(41)	-	(8961)	(428)	(402)
	Simuliidae							
1972	492	133	166	73				
	(278)	(84)	(145)	(49)				
1973	97	5	51	99				
	(45)	(3)	(20)	(59)				
1974	372	4	283	218				
	(318)	(2)	(94)	(99)				
1975	234	17	510	303				
	(153)	(11)	(150)	(250)				
1976	3646	38	232	452				
	(2395)	(10)	(134)	(405)				
1977	1332	646	125	37				
	(1192)	(590)	(67)	(23)				
1978	2250	1701	277	267				
	(1077)	(763)	(147)	(155)				
1979	1253	729	1406	102				
	(970)	(156)	(821)	(89)				
1980	11394	5808	1837	1317				
	(11331)	(2201)	(1124)	(298)				
1981	1173	796	568	690				
	(484)	(401)	(149)	(332)				
1982	495	1207	770	185				
	-	(631)	(643)	(177)				

Ephemerella doddsi, intolerant of sedimentation, are found in fast-flowing streams with high-quality water and clean substrates. Adults emerge May–July and early instar larvae appear July–September. Before construction of Electric Lake, this species was commonly found at Stations 4-UPH and D-4, but only rarely at Station 7-HSS and never at Station 12-HBM (Table 3). At Station 4-UPH, the *E. doddsi* population has shown no definite trend over the 11-year study period. Numbers dropped in 1977 due to low flows plus silts from upstream land use, but numbers in 1981 and 1982 were similar to those of 1972–1975. Sedimentation and low flows nearly eliminated *E. doddsi* from Station D-4 in 1974. Numbers were even lower in 1975 and no *E. doddsi* were collected at Station D-4 from 1976 to 1979. A few individuals were found in 1980 and 1982, but not in 1981. This may represent a gradual upstream migration, or some adults may be flying down canyon past Electric Lake and depositing their eggs at this station.

Ephemerella grandis larvae are crawlers/sprawlers inhabiting detritous and sand/gravel interstitial materials between larger rock substrates. Excessive amounts of sedimentation or algal growth can reduce population levels by clogging these interstices. Early instar larvae appear July–September and adults emerge June–August.

Ephemerella grandis was commonly found throughout the study area prior to 1974 (Table 3). At Stations 7-HSS and 12-HBM, numbers of *E. grandis* remained relatively stable during the study period. Numbers declined at Stations 4-UPH and D-4, both above and below the reservoir. Since Station 4-UPH is located near the top of the *E. grandis* elevational range, the population at Station 4-UPH was probably able to remain stable as long as adults could immigrate from downstream to lay their eggs. After Electric Lake filled, upstream movement of adults was largely blocked (Electric Lake is over 8 km long), and maintenance of population numbers is now mainly dependent upon success of local emergence, mating, and egg laying. Elimination of drift from upstream sites and reduction of habitat quality hampered recovery of *E. grandis* and kept numbers low at Station D-4 through 1980. Increased numbers in 1981 and 1982 could be in response to nearly normal spring flows in 1980 and 1982.

Pteronarcella badia are omnivorous, moss and detritous composing a major part of their diet, although macroinvertebrates are also eaten (Fuller and Stewart 1977). This species is a clinger or sprawler, common in streams below 2600 m elevation, and larvae are moderately tolerant to siltation and organic enrichment. Adults emerge and early instar larvae appear in spring and early summer with rapid larval growth immediately following hatching through fall. They overwinter as medium to large larvae.

Prior to impoundment, *P. badia* was found at every station below the dam site, but not at Station 4-UPH (Table 3). Numbers were higher and fluctuated less at Station 12-HBM than at the other stations. At Stations D-4 and 7-HSS, numbers have decreased since construction of Electric Lake Dam, probably the result of increased fine sediments and algal growth and decreased detrital matter in the stream. Night time oxygen demands of macrophytes, coupled with possible low DO water released from the dam, may have also stressed *P. badia*. Although *P. badia* are relatively tolerant to warm water temperatures and low DO when compared with other stoneflies, low DO levels, even if not lethal, could cause drift out of the area (Spence and Hynes 1971).

Two species of *Brachycentrus* are found in Huntington River: *B. americanus* and *B. occidentalis*. The two species are similar in appearance during larval stages, but can be differentiated by stages of development on date of collection.

Numbers of *Brachycentrus* fluctuated at each station in response to a variety of impacts. In 1976 numbers dropped, with the greatest reduction near the dam at Station D-4 (Table 3). Numbers remained low at Station D-4 through most of 1977, but increased by October and remained high through 1978 and into 1979. In July and August 1979, when *B. occidentalis* early instar larvae should have appeared in large numbers, no *Brachycentrus* were collected. In October, when *B. americanus* should have appeared, only 11 larvae were collected at Station D-4. Low numbers continued through 1980 until a new *B. americanus* hatch showed up in the November samples. Increased numbers were collected through June 1981, but no new larvae were collected in September, and numbers remained low throughout 1982. Total numbers of *Brachycentrus* at Station 7-HSS had noticable fluctuations, but remained high in comparison with Stations D-4 or 12-HBM.

As reported by Winget (1984b), both *B. americanus* and *B. occidentalis* have adaptations to help survive natural environmental extremes. *Brachycentrus americanus* adults emerge following spring high runoff. New instar larvae appear during late summer to early fall, and by spring, larvae are large enough to cope with high water velocities and associated sediment movements of runoff. *Brachycentrus occidentalis* emerge as adults in early spring so they are out of the stream during runoff, and larvae hatch from eggs beginning in July, just after runoff and at the start of a normally stable growing season.

Short-term flushing flows were released from Electric Lake between late July and the end of August, when early instar *B. occidentalis* larvae were present (Fig. 9). Small inorganic suspended sediments could have interfered with feeding and respiration, and small larvae were probably scoured off substrates by the moving sediments. It appears that, because of the July to August flushes, the summer hatching of *B. occidentalis* has proved a disadvantage in Huntington River below Electric Lake.

Widespread and common in cold, running, high-quality waters, *Arctopsyche grandis* live on tops and sides of rocks exposed to stream current (Wallace 1975). Using pieces of debris plus silk produced in glands near their mouths, larvae construct small shelters or "retreats." Nets adjoining their retreats have mesh sizes coinciding with water currents and age of the larvae (Merritt and Wallace 1981). Small animals and debris floating in the water are caught in these nets. Larvae will at times, especially in June, July, and August, become "agressive predators," leaving retreats to attack other macroinvertebrates (Mecom 1972).

A flood in June 1973 at Station D-4 caused severe scouring of the stream and eliminated larval *A. grandis*. During August and September of the same year, early instar *A. grandis* appeared in the samples. *Arctopsyche* are generally intolerant of sedimentation, but in this study numbers do not appear to correlate with measured levels of fine sediments. The probable explanation is that *Arctopsyche* build their nets in areas of swift currents where surfaces of substrates are kept relatively clean; and as Benke and Wallace (1980) reported, the numbers of *Arctopsyche* vary according to available food quantities in stream drift. Since completion of Electric Lake, numbers of chironomid midge larvae and *Baetis* mayflies, both active drifters and common prey of *A. grandis*, have increased dramatically. More food in the stream could help offset the negative effects of increased fine sediments, helping to maintain high numbers of *A. grandis* below Electric Lake. Benke and Wallace (1980) also reported that *Arctopsyche* are common in high numbers below impoundments.

Chironomidae as a family contain some of the most tolerant of aquatic insect species. Commonly called "midge flies," chironomids are found almost anywhere there is fresh water. Chironomids are tolerant to sedimentation, and increases in amounts of fine sediments often result in increased numbers of chironomids, especially if the fines are organically rich. In Huntington River, emergence of adults and subsequent laying of eggs appeared to occur almost year round, with major peaks in March to April and September to October.

Chironomid population densities at Station 4-UPH remained stable from 1972 to 1975, but, due to heavy watershed use and upstream construction (1975 to 1978), silt and nutrient levels increased with an associated increase in number of chironomids (Table 3). From 1978 to 1982 levels of fine sediments decreased (Fig. 6), as did chironomid densities. At Station D-4, below the dam, numbers increased beginning in 1974 and remained high throughout the remainder of the study. At Station 7HSS chironomid densities slowly increased through 1974 and remained high throughout 1981. Numbers dropped in 1982, possibly in response to increased spring flows removing accumulated fine sediments. Numbers of chironomids at Station 12-HBM appeared stable throughout the 11-year study period.

Simuliidae commonly appeared at every station. Simuliid larvae cling to the silken nets spun on substrate surfaces by the larvae and, using tiny featherlike appendages near their mouths, filter organic materials, including plankton, from passing water. Some species of Simuliidae are tolerant of organic enrichment and only slightly less tolerant of sedimentation. Simuliid larvae thrive where there is a steady supply of plankton or suspended organic detritus in the stream. Early instar simuliid larvae appeared in Huntington River from late spring throughout the summer, and adults emerged from July through October.

Following impoundment of Huntington River, simuliids increased in numbers at each of the stations sampled (Table 3). As a result of heavy sedimentation from construction and scouring affects from a flood, numbers at Station D-4 dropped in 1973 and remained low through 1976. Numbers increased in 1977 and remained high through 1982. At Station 7-HSS, numbers dropped in 1973, but have been high since, especially from 1979 to 1982, with numbers noticeably higher than in preimpoundment years.

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LITERATURE CITED

Barber, W. E., and N. R. Kevern. 1973. Ecological factors influencing macroinvertebrate standing crop distribution. Hydrobiologia 43:53–75.

Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net spinning caddisflies in a southern Appalachian stream. Ecology 61:108–118.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Vertag, New York, Inc. 253 pp.

Burns, J. W. 1970. Spawning bed sedimentation studies in northern California streams. California Fish and Game. 56:253–270.

Cordone, A. J., and D. W. Kelley. 1961. The influences of inorganic sediment on the aquatic life of streams. California Fish and Game 47:189–228.

Coutant, C. C. 1968. Effects of temperature on the development rate of bottom organisms. Pages 9.13–9.14 *in* Annual Report for 1967, USAEC Div. Biol. and Med. Batelle-Northwest, Richland, Washington.

Cummins, K. W. 1962. An evaluation of some techniques for the collection and ananlysis of benthic samples with special emphasis on lotic waters. Amer. Midl. Nat. 67:4774–504.

Elliott, J. M. 1971. Some methods for statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25. 144 pp.

Environmental Protection Agency. 1971. Algal assay procedures: bottle test. EPA, National Eutroph. Research Prog. Corvalis, Oregon.

Fuller, R. L., and K. W. Stewart. 1977. The food habits of stoneflies (Plecoptera) in the upper Gunnison River, Colorado. Environ. Ent. 6:293–302.

Gervais, B. 1975. Aquatic habitat studies of Huntington Creek. Manti-LaSal National For. (est. 1975), unpubl. rept.

Gore, J. A. 1977. Reservoir manipulations in a prairie river. Hydrobiol. 55:113–123.

———. 1978. A technique for predicting in-stream flow requirements of benthic macroinvertebrates. Freshwater Biol. 8:141–151.

———. 1979. Patterns of initial benthic recolonization of a reclaimed coal strip mined river channel. Canadian J. Zool. 57:2429–2439.

Hannan, H. H. 1979. Chemical modifications in reservoir-regulated streams. Pages 75–94 *in* J. V. Ward and J. A. Stanford, eds. The ecology of regulated streams. Plenum Publ. Corp.

Hansen, E. A. 1970. Sediment movement in a pool and riffle stream. IASH-UNESCO-Symposium on the Results of Research on Representative and Experimental Basins. [Wellington, New Zealand, December, 1970] Mimeograph, U. S. For. Ser.

Hilsenhoff, W. L. 1971. Change in the downstream insect and amphipod fauna caused by an impoundment with a hypolimnion dam. Ann. Ent. Soc. Amer. 64:743–746.

Humpesch, U. H., and J. M. Elliot. 1980. Effect of temperature on the hatching time of eggs of three *Rhithrogena* spp. (Ephemeroptera) from Austrian streams and an English stream and river. J. Anim. Ecol. 49:643–661.

Hutchinson, G. E. 1973. Eutrophication. Amer. Sci. 61:269–279.

Knopp, C. 1978. Huntington Creek flushing flows. Manti-LaSal National For., Unpubl. rept.

Kondratrieff, B. C., and J. R. Voshell, Jr. 1981. Influence of a reservoir with surface release on the life history of the Mayfly *Heterocleon curiosum* (McDonnough) (Ephemeroptera: Baetidae). Can. J. Zool 59:305–314.

Lehmkuhl, D. M. 1972. Change in thermal regime as a cause of reduction of benthic fauna downstream of a reservoir. J. Fish. Res. Bd. Canada. 29:1329–1332.

Lillenammer, A. 1975. Norwegian stoneflies. IV. Laboratory studies on ecological factors influencing distribution. Norwegian J. Entomol. 22:99–108.

Lowe, R. L. 1979. Phytobenthic ecology and regulated streams. Pages 25–34 *in* J. V Ward and J. A. Stanford, eds., The ecology of regulated streams. Plenum Publish. Corp.

McNeil, W. J. 1964. A method of measuring of pink salmon eggs and larvae. U.S. Fish & Wildl. Ser. Fish. Bull. 63, 3:575–588.

McNeil, W. J., and W. H. Ahnell. 1964. Success of pink salmon spawning relative to size of spawning bed materials. U.S. Fish and Wildl. Ser. Spec. Sci. Rept.— Fish. No. 469. 15 pp.

Mecom, J. O. 1972. Feeding habits of Trichoptera in a mountain stream. Oikos 23:401–407.

Merritt, R. W., and K. W. Cummins. 1978. An introduction to the aquatic insects of North America. Kendall Hunt Publ. Co. 441 pp.

Merritt, R. W., and J. B. Wallace, 1981. Filter feeding insects. Sci. Amer. 244:132–144.

Mulligan, H. F., and A. Baranowski. 1969. Growth of phytoplankton and vascular aquatic plants at different nutrient levels. Verh. Int. Ver. Limn. 17:802–810.

Nebeker, A. V. 1971. Effect of high winter water temperatures on adult emergence of aquatic insects. Water Res. 5:777–783.

Pfitzer, D. W. 1954. Investigations of waters below storage reservoirs in Tennessee. Trans. N. Amer. Wildl. Conf. 19:271–282.

Platts, W. S., and W. F. Megahan. 1975. Time trends in riverbed sediment composition in salmon and steelhead spawning areas: South Fork Salmon River, Idaho. 40th N. Amer. Wildl. and Natural Resources Conf. pp 229–239.

Porcella, D. B., and L. B. Merritt. 1976. Algal bioassay results on selected waters in the MAG Area. B Y U Environ. Anal. Lab., unpubl. rept., Brigham Young Univ., Provo, Utah. 5 pp.

Rees, D. M., and R. N. Winget. 1970. Current investigations in Utah of the biting gnat *Leptoconops kerteszi*. Mosq. News 30:121–127.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol & Ocean. 14:799–801.

Spence, J. A., and H. B. N. Hynes. 1971. Differences in benthos upstream and downstream of an impoundment. J. Fish. Res. Bd. Canada. 28:35–43.

Surber, E. W. 1937. Rainbow trout and bottom fauna production in one mile of stream. Trans. Amer. Fish. Soc. 66:193–202.

Vaughn Hansen Associates. 1980. Studies of natural waters in the Huntington Creek and Rock Canyon Creek basins. Unpubl. repts. Salt Lake City, Utah.

Wallace, J. B. 1975. The larval retreat and food of *Arctopsyche* with phylogenetic notes on feeding adaptations in Hydropsychidae larvae (Trichoptera). Ann. Ent. Soc. Amer. 68:167–173.

Ward, J. V. 1974. A temperature stressed stream ecosystem below a hypolimnial release mountain reservoir. Arch. Hydrobiol. 74:247–275.

_____. 1976a. Comparative limnology of differentially regulated sections of a Colorado mountain river. Arch. Hydrobiol. 78:314–342.

_____. 1976b. The effects of thermal constancy and seasonal temperature displacement on community structure of stream macroinvertebrates. Pages 302–307 *in* G. W. Esch and R. W. McFarlane, eds., Thermal ecology II., ERDA Symposium Series (CONF-750425).

Ward, J. V., and J. A. Stanford. 1979. Ecological factors controlling stream zoobenthos with emphasis on thermal modifications of regulated streams. Pages 35–36 *in* J. V. Ward, and J. A. Stanford, eds., The ecology of regulated streams. Plenum Publ. Corp.

Waters, T. F. 1969. Subsampler for dividing large samples of stream invertebrate drift. Limnol. and Oceanogr. 14:813–815.

Weber, C. I. 1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. National Environmental Research Center, Office of Research and Develop. U.S. E P A. Cincinnati, Ohio. 176 pp.

Williams, R. D., and R. N. Winget. 1979. Macroinvertebrate response to flow manipulation in the Strawberry River, Utah (U.S.A.). Pages 365–376 *in* J. V. Ward, and J. A. Stanford, eds., The ecology of regulated streams. Plenum Publ. Corp. 1980.

Winget, R. N. 1984a. Methods for determining successful reclamation of stream ecosystems. *In* J. E Gore, ed., Restoration of rivers and streams. Butterworth Pub. In press.

_____. 1984b. *Brachycentrus americanus* and *B. occidentalis* (Trichoptera) in a regulated stream. J. Freshwater Ecol. 2:373–381.

Winget, R. N., and F. A. Mangum. 1979. Biotic condition index: integrated biological, physical, and chemical stream parameters for management. U.S. Dept. of Agric. Intermntn. Reg. For. Ser., Oct. 1979. 51 pp.

FLORA OF THE LOWER CRETACEOUS CEDAR MOUNTAIN FORMATION OF UTAH AND COLORADO, PART II. *MESEMBRIOXYLON STOKESI*

G. F. Thayn[1] and W. D. Tidwell[2]

ABSTRACT.— *Mesembrioxylon stokesi*, sp. nov., from the Lower Cretaceous Cedar Mountain Formation of Utah is described and compared with other species of *Mesembrioxylon*. *Mesembrioxylon stokesi* is similar to Aptian members of this genus in having a combination of wood parenchyma and septate tracheids. This lends some support to the Cedar Mountain Formation being partially Aptian in age.

The Lower Cretaceous Cedar Mountain Formation is exposed throughout much of eastern Utah, western Colorado, and north central New Mexico (Young 1960). This formation is fossiliferous at several localities. Fisher et al. (1960) listed the formation as Aptian. It is still uncertain, however, whether it is Aptian, Albian, or both. Fossil plants reported from the Cedar Mountain Formation include *Tempskya* (Katich 1951, Stokes 1952, Tidwell and Hebbert 1972, Tidwell et al. 1976), cycadeoids (Furniss and Tidwell 1972), and dicotyledonous wood (Thayn et al. 1983). This paper is the first detailed report on coniferous woods from this formation.

The specimens of fossil woods consituting this report were collected from Molen Ridge, Emery County, Utah (Thayn et al. 1983). The Cedar Mountain Formation at this locality consists of a cap of coarse-grained, white sandstone that is underlain by channel fills of alternating yellow conglomeritic sandstone and grey-green shales. These beds are underlain by a dark green, nodular, weathering shale. The petrified logs at this site are highly

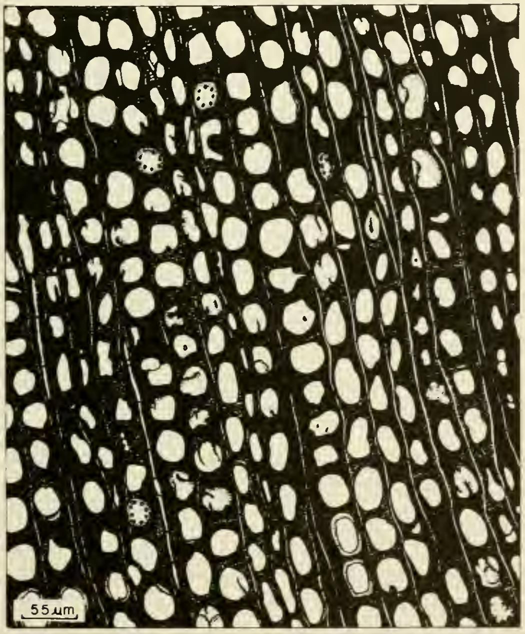

Fig. 1. Illustration of the transverse section showing distribution of axial parenchyma and general shape and arrangement of tracheids of *Mesembrioxylon stokesi* (Holotype).

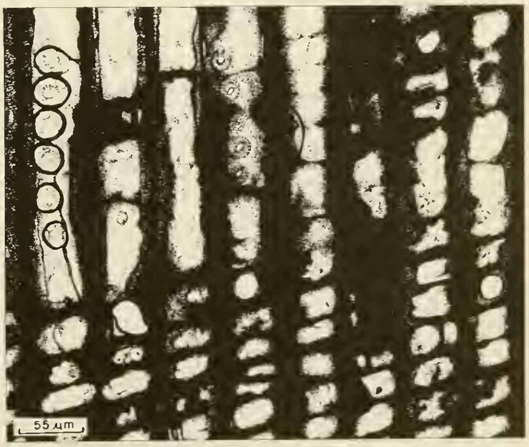

Fig. 2. Radial section showing the size and arrangement of radial tracheary pitting, presence of axial parenchyma, septations in the tracheids and the crossfields of *Mesembrioxylon stokesi* (Holotype).

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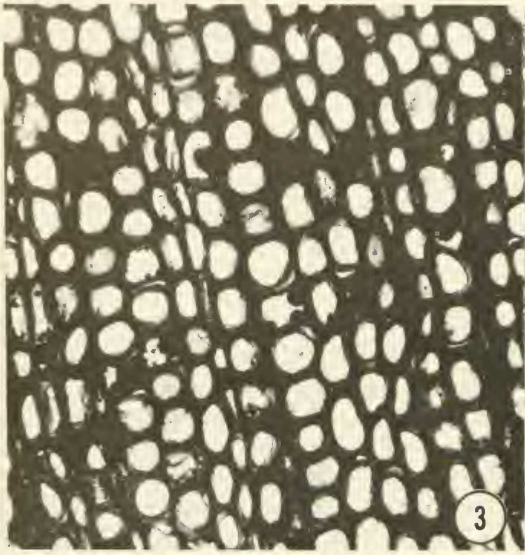

Fig. 3. Transverse section showing general shape and size of tracheids, diffuse axial parenchyma, and rays (250x) of *Mesembrioxylon stokesi* (Holotype).

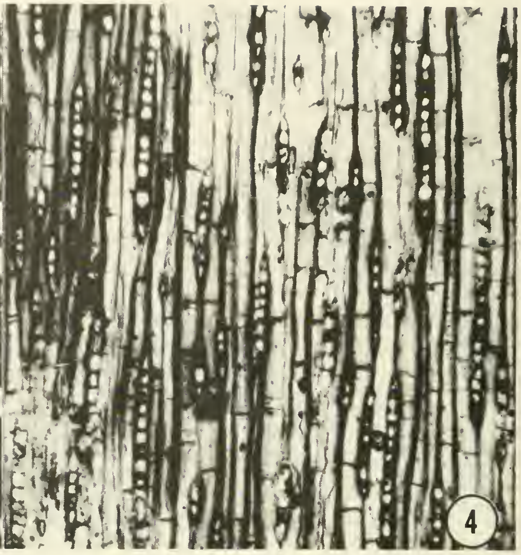

Fig. 4. Tangential section illustrating the abundance and size of the rays and ray cells (150x) of *Mesembrioxylon stokesi* (Holotype).

fragmented and lie on the surface of the yellow channel fills. Other coniferous woods, dicotyledonous woods, and *Tempskya* have also been collected at this site.

Mesembrioxylon stokesi, sp. nov.

DESCRIPTION AND DIAGNOSIS.— Growth rings indistinct with only a few layers of late wood cells; ring width varies 1.3–9.2 mm; transition from early to late wood gradual. Tracheids square, rectangular or oval in outline, with walls 7–10 μm; tracheid size ranges from 18 μm and isodiametric to 55 μm radial diameter by 18 μm tangential diameter; intercellular space common in late wood. Tracheids septate; radial tracheary pitting uniseriate, generally separate but occasionally vertically contiguous, circular bordered pits 10–19 μm in diameter. Pit apertures either circular or elliptic and small (3 μm) in relation to the size of the pit; crassulae lacking. Tangential pitting not apparent. Axial parenchyma abundant, 12–60 cells/mm^2. Parenchyma resinous, filled with dark cell contents. Axial parenchyma cells 40–210 μm high and up to 35 μm in diameter with 2–3 μm thick walls. Rays abundant, 9–14/tangential mm; 1–8 (ave. 4) rows of tracheids between the rays. Rays entirely parenchymatous; marginal cells wavy in outline. Rays uniseriate to partially biseriate, 1–50 (generally 8–16) cells (870 μm) high. Horizontal and tangential walls of ray cells smooth to slightly nodular and 2–3 μm thick (common wall). Ray cells square to rectangular; 35–125 μm radial diameter, 8–35 μm both tangential and vertical diameter. Crossfield pitting of two types; generally one podocarpoid pit per crossfield or very rarely 1–3 small bordered pits with slitlike apertures. Pits up to 18 μm in diameter, generally with broad border and with elliptic to square-oblong apertures, rarely thin borders with diagonally or vertically oriented elliptic apertures that range 3–9 μm at the widest point. Small crossfield pits approximately 4–8 μm in diameter with slitlike apertures.

Repository: Brigham Young University 2192 (Holotype).

Locality: Molen Ridge (Ferron Site) 9 miles east of Ferron, Utah (U.S. Geol. Surv.: Desert Lake Quadrangle NE, SW, Sec. 23, T20S, R8E).

Horizon: Lower Cretaceous Cedar Mountain Formation.

AFFINITIES.— The most characteristic feature of *Mesembrioxylon stokesi* is the large

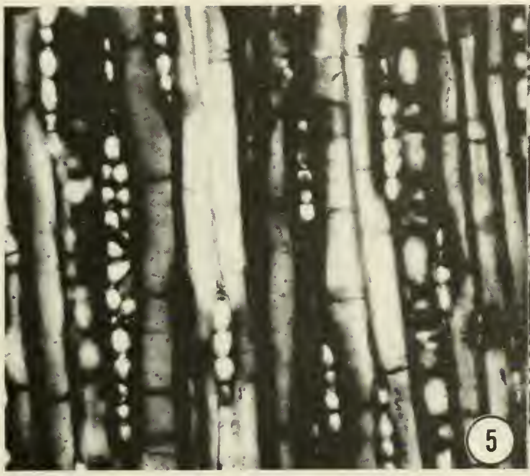

Fig. 5. Tangential section showing axial parenchyma, a partially biseriate ray and numerous septations in the tracheids (250x) of *Mesembrioxylon stokesi* (Holotype).

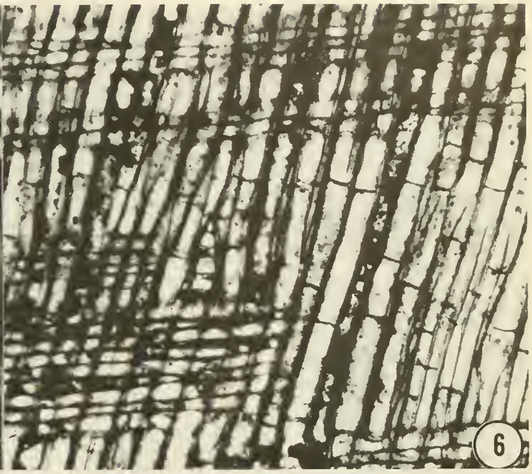

Fig. 6. Radial section demonstrating axial parenchyma; septate tracheids, crossfield pitting, and relative size of ray cells (153x) of *Mesembrioxylon stokesi* (Holotype).

open pits seen in the crossfields. Among extant woods this type of pitting occurs in several members of the Podocarpaceae and in the genera *Juniperus* (Cupressaceae), *Pinus* (Pinaceae), and *Sciadopitys* (Taxodiaceae). In 1905 Gothan proposed the name *Phyllocladoxylon* for petrified conifer wood that lacks resin canals and wood parenchyma but has one simple ray pit (phyllocladoid) per crossfield and separate circular bordered pits on the tracheids. The name *Podocarpoxylon* was also established by Gothan (1905) for fossil conifer wood with wood parenchyma and bordered crossfield pits with large elliptic apertures (podocarpoid pits). Stopes (1915) combined Gothan's genera into *Podocarpoxylon* pointing out that the two could not be distinguished on the basis of the crossfield pitting since both types of pits occur in the various species of both *Podocarpus* and *Phyllocladus*. Seward (1919) established the genus *Mesembrioxylon* because he thought, when there is no evidence of affinity with any particular living genus, a name free from implication should be used.

Krausel (1949) maintained a distinction between *Phyllocladoxylon* and *Podocarpoxylon* also on the basis of the crossfield pitting. He defined *Podocarpoxylon* as having small crossfield pits with vertical to steeply inclined apertures, whereas *Phyllocladoxylon* was to have large crossfield pits with oblique-elliptic apertures. Nevertheless, Bhardwaj (1953), Ramanujam (1953), Jain (1964), and Nishida (1966) all retained Seward's *Mesembrioxylon*.

About 30 species have been described as *Mesembrioxylon*, *Phyllocladoxylon*, or *Podocarpoxylon*. All but four of these species differ from *M. stokesi* by having different combinations of ray height, size and number of crossfield pits, axial parenchyma, configuration of tracheary pitting, and lack of septations in the tracheids (Table 1).

Mesembrioxylon woburnense (Stopes) Seward (1919) resembles *M. stokesi* in having rays varying from 1 to over 40 cells high and are occasionally partially biseriate. It differs in lacking septations in the tracheids and by having 1 or 2 pits in the crossfield that are in one horizontal row. It also has crassulae that are lacking in *M. stokesi* and radial tracheary pitting that is occasionally in two opposite rows rather than exclusively uniseriate.

Of the described species of *Mesembrioxylon* only *M. nihei-takagi* Nichida (1966) and *M. gothani* (Stopes) Seward (1919) have a combination of septate tracheids and wood parenchyma similar to *M. stokesi*. *Mesombrioxylon nihei-takagi* has rays up to 10 cells high that are uniseriate or partially biseriate and parenchyma in tangential bands. *M. stokesi* has rays up to 50 cells high that are uniseriate or partially biseriate and diffuse wood parenchyma. *Mesembrioxylon gothani*, as originally described by Stopes (1915), has rays of 1–8 cells high that are exclusively uniseriate and scattered wood parenchyma. Shimakura (1937) reported a specimen of this species that had rays up to 18 cells high. *Mesembrioxylon stokesi*, however, has higher rays that are partially biseriate. *Mesembrioxylon stokesi* has a ray structure similar to *M. woburnense* and septate tracheids and crossfield pitting like *M. gothani*. Thus, *M. stokesi* appears to be a new species intermediate between the two.

Xenoxylon morrisonense Medlyn and Tidwell (1975) from the Upper Jurassic Morrison Formation, which underlies the Cedar Mountain Formation, is anatomically very close to *Mesembrioxylon stokesi*. They are similar in that both have septate tracheids and large podocarpoid crossfield pits. These species differ in that *M. stokesi* has broad borders on its podocarpoid pits as compared with the narrow borders in *X. morrisonense*. *M. stokesi* has smooth horizontal and end walls in its ray parenchyma and numerous resin cells, and its few contiguous bordered pits are not flattened as in *X. morrisonense*, a feature characteristic of most *Xenoxylon* species. Horizontal and end walls of ray parenchyma in *X. morrisonense* have numerous indentations and it lacks resin in any of its cells.

Protocedroxylon scoticum (Holden) Seward (1919) is also similar to *Mesembrioxylon stokesi*. However, *P. scoticum* has araucarian pitting (Holden 1915), which is lacking in *M. stokesi*.

The specific epithet of *Mesembrioxylon stokesi* is given in honor of Dr. William Lee Stokes of the University of Utah, who first collected specimens of fossil wood from the Molen Ridge site.

Stratigraphic relationships.— It is not presently known whether the Cedar Mountain Formation is Aptian or Albian in age. The presence of dicotyledonous woods in the formation (Thayn et al, 1983) possibly makes

Table 1. Comparison of *Mesembrioxylon stokesi* with similar species.

Species	Ray height	Tracheid septations	Radial pit size	Crossfield pitting	Axial parenchyma	crassulae	Size and shape of Tracheids (x-sec)
M. stokesi	1–18 to over 50	thick walled	circular 10–19 μm	one large podocarpoid pit with broad borders, having 1–3 small border pits with lenticular apertures	abundant and diffuse	lacking	square or radially elongate 18 x 18 to 18 x 55 μm
M. gothani	1–8, mostly 3 cells high (1–18 in Shimakura, 1937)	thin and horizontal	circular or ovoid, 15–17 μm celliptical pits	one or two 7 μm ovoid, circular or	sparse and diffuse	lacking	various, 20–25 μm
M. nihei-takagi	1–4, rarely 8 cells high thin and horizontal	thin and ovoid, 8–10 μm	circular or three, 5–8 μm	one to and diffuse	abundant	lacking	tangentially elongate 15–22 μm
M. woburnense	4–10, up to 35 cells high (over 40 in Shimakura, 1937)	lacking	circular, 9–15 μm	one to two in a horizontal row zontal row 10–15 μm	10–15 μm zonate	sparse and	present rectangular to radially elongate, 30–39 μm

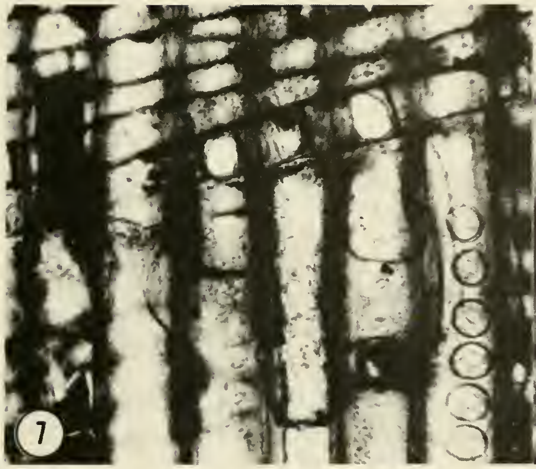

Fig. 7. Radial section showing two types of crossfield pits and circular radial tracheary pits (500x) of *Mesembrioxylon stokesi* (Holotype).

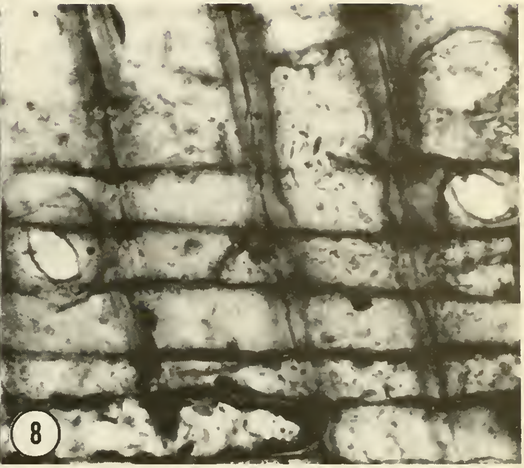

Fig. 8. Closeup of radial section of ray. Note the broad borders on the crossfield pits (1000x) of *Mesembrioxylon stokesi* (Holotype).

it Albian since reported Aptian dicotyledonous woods have been placed in doubt by Wolfe et al. (1975). *Mesembrioxylon* ranges from the Permian to the Pliocene, but the woods most comparable to *M. stokesi* were first collected from sediments reported as Aptian. *Mesembrioxylon gothani* and *M. woburnense* have been collected from the Aptian of England (Stopes 1915) and Japan (Nishida 1966). However, Shimakura (1937) reported both species from the Upper Cretaceous of Japan and *M. woburnense* was reported from the Tertiary of India (Ramanujam 1953). The only other species of *Mesembrioxylon* with septate tracheids and partially biseriate rays is *M. nihei-takagii* which was collected from the Aptian of Japan (Nishida 1966).

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LITERATURE CITED

BHARDWAJ, D. C. 1953. Jurassic woods from the Rajmahal Hills, Bihar. The Palaeobot. 2:59–70.

FISHER, D. J., C. E. ERDMAN, AND J. B. REESIDE. 1960. Cretaceous and Tertiary formations of the Book Cliffs, Carbon, Emery, and Grand Counties, Utah, and Garfield and Mesa counties, Colorado. U.S. Geol. Surv. Prof. Paper 332. 1–80.

FURNISS, B., AND W. D. TIDWELL. 1972. Cycadeoidales from the Cedar Mountain Formation near Moab, Utah. Geol. Soc. Amer. (Abstr.) 4(6):377.

GOTHAN, W. 1905. Zur anatomic lebender und fossiler Gymnopsermem-Holzer. Abh. K. Preuss. Geol. landes. 44:1–108.

HOLDEN, R. 1915. A Jurassic wood from Scotland. New Phyt. 14:205–209.

JAIN, K. P. 1964. A new species of *Mesembrioxylon*, *M. rasmahalense* from the Rajmahal Hills, Bihar, India. The Palaeobot. 13(2):153–154.

KATICH, P. J. 1951. Occurrence of *Tempskya* in the Lower Cretaceous of the Western Interior. J. Paleon., 26(4):677.

KRAUSEL, R. 1949. Die fossilen Koniferenholzer (unter Asschluss von *Araucarioxylon* Kraus) II. Tiel. Kritische untersuchungen zur diagnostik lebender und fossiler Koniferenholzer. Palaeontographica 89B:83–203.

MEDLYN, D. A., AND W. D. TIDWELL. 1975. Conifer wood from the Upper Jurassic of Utah, Part I: *Xenoxylon morrisonense*. Amer. J. Bot. 62(2):303–309.

NISHIDA, M. 1966. On some petrified plants from the Cretaceous of Choshi, Chiba Prefecture III. Bot. Mag. Tokyo 79:226–235.

RAMANUJAM, C. J. K. 1953. On two species of *Mesembrioxylon* from the vicinity of Pondicherry, South India. The Palaeobot. 2:101–106.

SEWARD, A. C. 1919. Fossil Plants. Vol. IV. Cambridge Univ. Press, London 543 pp.

SHIMAKURA, M. 1937. Studies on fossil woods from Japan adjacent lands II. The Cretaceous woods from Japan, Saghalien and Manchoukuo. Sci. Rep. Tohok. Imp. Univ. Sendai, Ser. 2, 19(1):1–73.

Stokes, W. L. 1952. Lower Cretaceous in Colorado Plateau. Amer. Assoc. Pet. Geol. Bull. 36(9):1774–1796.

Stopes, M. C. 1915. Catalogue of Mesozoic plants in the British Museum (Nat. Hist.). London. Pt. II:1–360.

Thayn, G. F., W. D. Tidwell, and W. L. Stokes. 1983. Flora of the Lower Cretaceous Cedar Mountain Formation of Utah and Colorado. Part I. *Paraphyllanthoxylon utahense*. Great Basin Nat. 43(3):294–402.

Tidwell, W. D., and N. Hebbert. 1972. *Tempskya* from the Cedar Mountain Formation near Moab. Geol. Soc. Amer. (Abstr.) 4(6):417–418.

Tidwell, W. D., G. F. Thayn, and J. L. Roth. 1976. Cretaceous and Early Tertiary floras of the Intermountain Area. Brigham Young Univ. Geol. Studies 22:77–98.

Wolfe, J. A., Doyle, J. A., and V. M. Page. 1975. The bases of angiosperm phylogeny: Paleobotany. Ann. Mo. Bot. Gard. 62:801–824.

Young, R. G. 1960. Dakota Group of Colorado Plateau. Amer. Assoc. Pet. Geol. Bull. 44(1):156–194.

NEW *ASTRAGALUS* (LEGUMINOSAE) FROM THE GOOSE CREEK DRAINAGE, UTAH – NEVADA

N. Duane Atwood[1], Sherel Goodrich[2], and Stanley L. Welsh[3]

Abstract.— A new species, *Astragalus anserinus* Atwood, Goodrich, & Welsh, is described from specimens taken from tuffaceous outcrops in the Goose Creek drainage of Box Elder County, Utah and Elko County Nevada.

A distinctive small-flowered species of *Astragalus* (Fig. 1.) was taken from tuffaceous outcrops in the Goose Creek drainage of Box Elder County, Utah, and adjacent Elko County, Nevada. Affinities of this handsome dwarf and matted species apparently lie with the section Argophylli. Within that section, because of the tiny flowers, they would appear to be allied to *A. subvestitus* Barneby, a species of moderate elevations in Tulare and Kern counties, California. The plants are villous-tomentose and shortly caulescent. The valves of the thinly villous pods are apparent through the vestiture. In shape they are nearly identical with pods of varieties within *A. purshii*, being dorsiventrally compressed and curved in such a manner that the beak lies almost parallel with the base of the pod. The pods are strictly unilocular, with no apparent septum within the locules of those examined.

The tiny flowers are unique in the section, being 9–11.2 mm long, which is smaller than those reported for *A. subvestitus*.

***Astragalus anserinus* Atwood, Goodrich, & Welsh,** sp. nov. Affinis dubius sed similis *Astragalo subvestito* Barneby in floribus parvis et pilis sparsis sed in floribus parvioribus et semina paucioribus differt.

Dwarf, tufted or matted, shortly caulescent, perennial herbs from a slender taproot; stems 3–11 cm long, decumbent-spreading; herbage villous-tomentose; stipules all free; leaves 1–4 cm long; leaflets 5–15, 3.2–6.5 mm long, obovate; peduncles 1.1–2.4 cm long; racemes with 3–7 flowers, the axis 1–5 mm long, little if at all elongating in fruit; bracteoles lacking; bracts ca 2 mm long, lance-subulate; pedicels 0.6–1.2 mm long; calyx tube 3.6–4.8 mm long, the teeth 1.1–1.8 mm long, subulate; flowers 9–11.2 mm long, pink-purple; pods sessile, 9–12 mm long, 5–7 mm wide, deciduous from within the calyx; dorsiventrally compressed, falcately curved, conspicuously trigonous-beaked, thinly vil lous; ovules 16–20; seeds 1.2 mm long.

Type: USA. Utah. Box Elder Co., T14N, R19W, S15 (SE1/4), 22 km NW of Lynn, Goose Creek drainage, 6.5 km S of Utah-Idaho line, white tuffaceous sand, nearly barren slope along a wash, 23 June 1982, D. Atwood and S. Goodrich 8989 (Holotype BRY; isotypes NY, POM, US, RM, UTC).

Additional specimens: Utah. Box Elder Co., 22.5 km NW of Lynn, 23 June 1982, D. Atwood & S. Goodrich 8990 (BRY, UT,UTC,NY); ca 25.5 km NW of Lynn, Goose Creek, ca 0.5 km due E of Utah-Nevada line, 23 June 1982, D. Atwood & S. Goodrich 9000 (BRY,NY,US); Utah-Nevada line at the Hardister VABM, 7 km S of Idaho line, 23 June 1982, D. Atwood & S. Goodrich 9004 (BRY); Nevada. Elko Co., T47N, R70E, S29 (SW1/4), 6 km S of Idaho on the Utah-Nevada line, D. Atwood & S. Goodrich 9002 (BRY,ID,M0,NY,RENO,RM,US).

Literature Cited

Barneby, R. C. 1964. Atlas of North American *Astragalus*. Mem. New York Bot. Gard. 13:597–1188.

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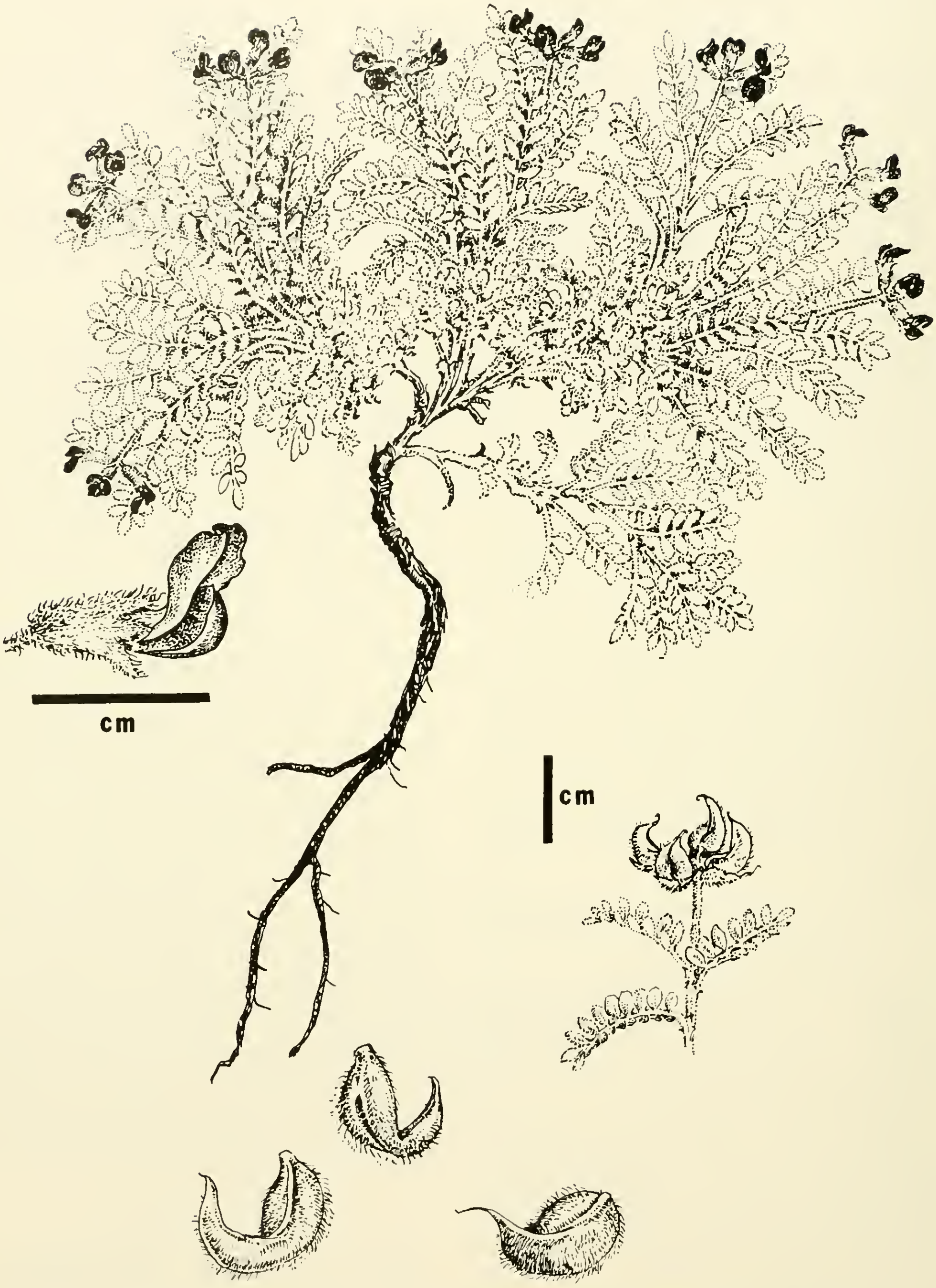

Fig. 1. Habit and details of *Astragalus anserinus* Atwood, Goodrich, and Welsh (Drawing by Kay Thorne).

SOME EDAPHIC RELATIONS OF SOUTHEASTERN IDAHO WILDLANDS[1]

Mark E. Jensen[2]

Abstract.— Soil samples from the A1 horizon and dominant subsoil horizon at 190 sites were analyzed for Ca, Mg, K, P, and organic matter contents in conjunction with a soil resource inventory of the Caribou National Forest. Vegetative composition and production data were compared to the edaphic factors to derive relationships useful to the land manager. Organic matter was effective in distinguishing between soil orders and was positively correlated to vegetative production. Vegetative cycling of the nutrients P and K was most pronounced in soils of the order Mollisols, to a lesser degree in the Alfisols, and not at all in the Entisols. The K/Mg ratio of the soil showed a negative correlation to grass production and a positive correlation with shrub production. An interpretative table is provided to aid determinations of high versus low values for the edaphic factors studied.

Soil scientists of the Intermountain Region, U.S. Forest Service, are commonly required to provide the land manager information concerning the soils management potential. Such information is usually based solely upon soil morphological features due to the lack of soil nutrient data available for wildlands of this region.

The primary objective of this study was to determine modal values for some soil nutrients within the soil groups of the Caribou National Forest, southeastern Idaho. Such information is needed if future collection of soil nutrient data on such lands is to have a basis for comparison. A secondary objective was to determine what relationships exist between nutrient levels in the soil and vegetative production and composition.

Study Area

The Caribou National Forest is located in southeastern Idaho, covering an elevational range of 1490 to 2930 m (Fig. 1). It occurs mainly within the Middle Rocky Mountain physiographic province, with some inclusion of the Basin Range physiographic province (Fenneman 1931). The geology is complex, ranging from Precambrian metamorphics in the Bannock and Portneuf ranges to Jurassic-Triassic sedimentaries in the Bear River and Webster ranges to Cretaceous sedimentaries in the Caribou Range.

Baily (1980) has classified the vegetation of the Caribou National Forest as belonging to the Rocky Mountain Forest Province, Douglas-Fir Forest section and the Intermountain Sagebrush–Wheatgrass section. The climate is a semiarid steppe regime with a wide range in mean annual precipitation. The lower elevations receive 330 mm of precipitation per year, and the higher elevations receive 1524 mm annual precipitation. Approximately 60% of the precipitation on the area is in the form of snow. Elevation and aspect exert a strong influence on growing season, with microclimatic variables playing a dominant role in determining the vegetative composition and production on sites.

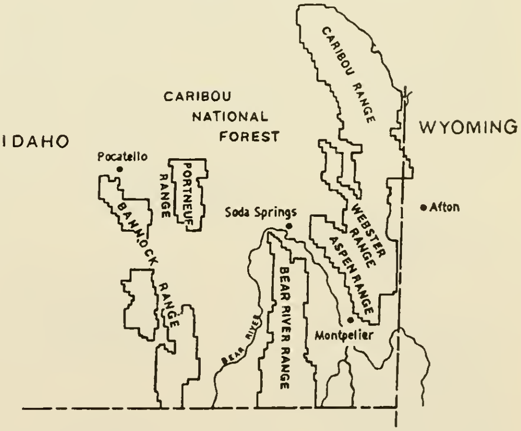

Fig. 1. The Caribou National Forest in southeastern Idaho.

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[1] Contributed by the Caribou National Forest, Pocatello, Idaho.

[2] Humboldt National Forest, Elko, Nevada 89801.

METHODS

Between 1975 and 1981 a soil resource inventory was conducted on approximately 485,640 ha of the Caribou National Forest. An order 3 soil survey was used in identifying landtypes as the mapping units (Wertz 1972). This is a broad level reconnaissance survey that utilizes the factors of soil formation (Jenny 1961) to identify the soils of the mapping unit. One hundred thirty landtypes with an average size of 259 ha were mapped. The modal soils of the mapping units were identified to family level utilizing the guidelines of *Soil Taxonomy* (USDA 1975). Composition of soil subgroups analyzed for nutrient content are presented in Table 1. Sampling was designed to cover the full range of dominant soils encountered.

Samples of the Al horizon and the dominant subsoil horizon (argillic or cambic horizon for the soil orders Mollisols and Alfisols and the C horizon for the soil order Entisols) were collected, air dried in the lab, and crushed before sieving through a 2-mm screen. Soil organic matter was determined by the Walkley-Black method, and available phosphorus (P) was determined by the Dilute Acid-Flouride method (Black 1965). Soil nutrients [potassium (K), magnesium (Mg) and calcium (Ca)] were determined in liquid solutions drawn from soil-water slurries having a ratio of 1 to 2. Slurries were agitated for 12 hours on a mechanical shaker. The resultant soil paste was transferred to a Buchner filter for extraction of a sediment-free filtrate. One to two drops of sodium hexametaphosphate were added to each extract to prevent the precipitation of $CaCO_3$. Levels of K, Mg, and Ca were determined from the filtrate in parts per million by use of an atomic absorption spectrophotometer.

Vegetative information was collected by the site analysis and ocular methods used by Intermountain Region Forest Service range personnel (USDA 1969). Composition values provided by these methods are estimates of the percentage of the total production contributed by each species on a site. All statistical tests followed Zar (1974).

TABLE 1. Composition of the soil mosaic of the Caribou National Forest.

Soil subgroups	Relative extent of the Caribou N.F. (% by area)
Argic Pachic Cryoborolls	10
Cryic Pachic Paleborolls	2
Pachic Cryoborolls	5
Argic Cryoborolls	18
Typic Cryoborolls	10
Typic Argixerolls	1
Typic Haploxerolls	2
Mollic Cryoboralfs	7
Typic Cryoboralfs	3
Typic Cryorthents	5
Typic Xerorthents	1

RESULTS AND DISCUSSION

Soil Groupings

A total of 26 soil families were analyzed in this study (Table 2). A high proportion (about 78%) of the soils studied were from the Mollisol soil order. These soils tend to support most of the highly productive rangeland sites on the study area. The Alfisol soil order is commonly associated with timber sites, but occasionally support rangeland. Entisols are highly variable, with some commercial-size timber and some lower-production-potential rangeland. Entisols are often associated with hill slopes of high runoff potentials and are commonly managed for watershed values on the study area.

In making comparisons between soil families, it was necessary to group some families to higher levels of the soil classification system, due to limited sample size. *Soil Taxonomy* provides a hierarchical classification system that allows for the grouping of soils from lower to higher categories. In making such groupings, increased variability is introduced into the sample of soils; yet it is still possible to make reasonable predictions about responses to management and manipulation within the higher soil groupings.

Edaphic Factors

Edaphic factors offer criteria for making distinctions between the soil groupings (Table 3). In particular, the Mollisols, Alfisols, and Entisols possess noticeable differences in soil nutrients. The Mollisols exhibited the highest overall mean values for the nutrients studied, followed by Alfisols. Entisols showed the lowest levels. This is consistent with genesis processes involved with development of these soils (USDA 1975).

A Newman-Keul multiple range test for unequal sample size was performed on the data to examine if significant differences in mean values existed (Zar 1974). The three soil orders differed significantly in respect to organic matter in the Al horizon (Table 4).This result is as expected, in that soil organic matter is controlled by long-term vegetative production and species composition on a site. These factors in turn affect soil development. Phosphorus also showed significant differences between soil orders, but K, Mg, and Ca did not.

Table 5 presents an interpretive guide for some plant nutrient levels in the soils studied. The values reported can be used to determine whether new Al horizon nutrient values are unusual. The levels reported are based on means and standard deviations for samples taken from each soil order on the Caribou National Forest. Caution is suggested in applying these relations to soils and site conditions significantly different from those of this study.

Nutrient Cycling Relations

The degree of nutrient cycling within Mollisols, Alfisols, and Entisols was studied. The nutrients P and Mg were analyzed with respect to concentrations in the Al and the subsoil of selected profiles. If P and Mg were not being cycled by vegetation, one would expect higher levels of both elements in the subsoil horizon sampled. Table 6 shows that both P and Mg are being rapidly pumped from subsoil to Al horizons in Mollisol soils. Magnesium is significantly more concen-

TABLE 2. List of soil families considered with associated vegetation types and sample size.

Soil family	Associated vegetation types	Sample size
	Order Mollisols	
Fine, mixed, Argic Pachic Cryoborolls	Aspen, Mountain Brush, Sage-Grass	4
Fine loamy, mixed, Argic Pachic Cryoborolls	Aspen, Mountain Brush, Sage-Grass	24
Clayey skeletal, mixed, Argic Pachic Cryoborolls	Aspen, Mountain Brush, Sage-Grass	3
Loamy, skeletal, mixed, Argic Pachic Cryoborolls	Aspen, Mountain Brush, Sage-Grass	4
Fine loamy, mixed, Cryic Pachic Paleborolls	Mountain Brush, Sage-Grass, Dry Meadow	8
Fine loamy, mixed, Pachic Cryoborolls	Aspen, Mountain Brush, Sage-Grass	4
Coarse loamy, mixed, Pachic Cryoborolls	Aspen, Mountain Brush, Sage-Grass	4
Loamy skeletal, mixed, Pachic Cryoborolls	Aspen, Mountain Brush, Sage-Grass	4
Fine, mixed, Argic Cryoborolls	Sage-Grass, Forb	12
Fine loamy, mixed, Argic Cryoborolls	Mountain Brush, Sage-Grass	19
Loamy skeletal, mixed, Argic Cryoborolls	Mountain Brush, Sage-Grass	24
Fine loamy, mixed, Typic Cryoborolls	Sage-Grass	3
Loamy skeletal, mixed, Typic Cryoborolls	Mountain Brush, Sage-Grass	12
Fine loamy, mixed, mesic, Typic Argixerolls	Juniper, Mountain Brush, Sage-Grass	10
Loamy skeletal, mixed, mesic, Typic Argixerolls	Juniper, Mountain Brush, Sage-Grass	5
Loamy skeletal, mixed, mesic, Typic Haploxerolls	Juniper, Mountain Brush, Sage-Grass	8
	Order Alfisols	
Fine, mixed, Mollic Cryoboralfs	Pine, Fir, Mountain Brush	5
Fine loamy, mixed, Mollic Cryoboralfs	Pine, Fir, Mountain Brush	6
Loamy skeletal, mixed, Mollic Cryoboralfs	Pine, Fir, Mountain Brush	3
Fine loamy, mixed, Typic Cryoboralfs	Pine, Fir	6
Loamy skeletal, mixed, Typic Cryoboralfs	Pine, Fir	4
	Order Entisols	
Fine loamy,mixed, Typic Cryorthents	Pine, Fir, Sage-Grass	4
Loamy skeletal, mixed, Typic Cryorthents	Pine, Fir, Sage-Grass	4
Fine loamy, mixed, mesic, Typic Xerorthents	Juniper, Sage-Grass	4
Loamy skeletal, mixed, mesic, Typic Xerorthents	Juniper, Sage-Grass	4
Sandy skeletal, mixed, mesic, Typic Xerorthents	Juniper, Sage-Grass	3

trated in the Al than in the subsoil of Alfisols, and, although P shows a strong trend in the same direction, the difference is not statistically significant. There is only a slight hint of nutrient pumping in the Entisols considered here. A Wilcoxon paired sample test was used to determine if the nutrient contents of the horizons represented different populations (Zar 1974).

The data suggest (Table 6) that vegetation on Mollisols (aspen, mountain brush, and sage-grass types) are effective in cycling nutrients each year from the subsoil to the surface. Such data have relevance for recommendations frequently made by forest soil scientists to stockpile top soil before initiation of site-disturbing activities. Top soil is widely valued for its beneficial physical and chemical properties for site reclamation (Brady 1974). My results suggest that top soil storage would be highly desirable for Mollisols and probably for Alfisols as well, but the practice could hardly be justified for the Entisols considered here.

Soil Taxonomy Implications

Soil organic matter appears to be the best indicator of soil variability and potential of

Table 3. Nutrient values for Al horizons by various soil groupings.

Soil group	P(ppm)	Ca(ppm)	K(ppm)	Mg(ppm)	Organic matter (%)	Production°	Mollic Epipedon depth°°
Fine and fine loamy families of Argic Pachic Cryoborolls	n = 43	27	27	35	43	43	43
	x̄ = 48.6	17.3	11.2	14.9	5.1	1,882	53.6
	s = 14.3	11.2	11.7	9.6	1.2	446	11.3
Fine and fine loamy families of Pachic Cryoborolls	n = 12	10	11	11	11	11	11
	x̄ = 46.8	20.9	16.8	14.4	5.4	1,634	49.9
	s = 20.5	20.6	13.6	10.8	1.5	440	14.9
Fine family of Argic Cryoborolls	n = 12	8	8	12	12	12	12
	x̄ = 47.7	10.0	12.9	13.3	4.9	1,123	26.8
	s = 16.9	5.9	5.0	8.1	1.2	293	5.0
Fine loamy family of Argic Cryoborolls	n = 19	8	8	16	21	19	19
	x̄ = 46.4	16.1	13.8	18.6	4.9	1,382	29.7
	s = 16.9	9.8	7.7	13.1	1.2	276	4.9
Loamy skeletal family of Argic Cryoborolls	n = 24	18	19	20	22	24	24
	x̄ = 45.6	17.6	18.1	12.8	4.5	1,260	29.8
	s = 19.6	10.0	13.8	3.9	1.1	383	4.8
Fine and fine loamy families of Typic Cryoborolls	n = 15	8	9	12	15	15	15
	x̄ = 29.9	24	23.8	11.4	4.5	968	27.9
	s = 21.0	15.6	21.4	7.1	1.4	333	7.6
All Argic Cryoborolls	n = 55	34	35	48	55	55	54
	x̄ = 46.3	15.5	15.9	14.8	4.7	1,284	29.0
	s = 17.8	9.4	11.2	9.1	1.2	348	4.9
All Xerolls	n = 23	10	11	19	23	23	23
	x̄ = 23.4	29.4	9.2	15.0	4.1	859	29.5
	s = 18.1	32.7	7.8	12.0	1.1	255	4.8
All Alfisols	n = 22	19	21	24	23	—	—
	x̄ = 53.4	13.0	14.4	10.4	3.2	—	—
	s = 15.9	11.2	11.6	4.6	1.6	—	—
All Entisols	n = 19	13	11	17	19	—	—
	x̄ = 21.3	14.4	6.2	9.0	2.4	—	—
	s = 20.7	10.5	8.4	6.9	1.1	—	—
All Mollisols	n = 148	89	93	124	143	147	148
	x̄ = 41.8	19.0	14.6	14.5	4.8	1,449	37.6
	s = 19.7	16.2	13.0	9.7	1.3	889	14.3

n = sample size
x̄ = mean
s = standard deviation

° = kg/ha/yr dry weight
°° = cm

Table 4. A comparison of mean nutrient values of the Al horizon by soil order.

Soil order	P(ppm)	Ca(ppm)	K(ppm)	Mg(ppm)	Organic matter (%)
Mollisols	41.8^a	19.0^a	14.6^a	14.5^a	4.8^a
Alfisols	53.4^b	13.0^a	14.4^a	10.4^b	3.2^b
Entisols	21.3^c	14.4^a	6.2^b	9.0^b	2.4^c

Note: Means having the same letter in superscript do not differ significantly as determined by the Newman-Keul multiple range test for unequal sample sizes interpreted at the 95% confidence level.

the edaphic factors studied. Organic matter was found to be the most useful variable in distinguishing between soil orders, as well as Mollisol subgroups.

A criterion used in defining Mollisols is organic matter content of the mollic epipedon (USDA 1975). Specifically, the organic matter content of the mollic epipedon must be 1% or more throughout its thickness. The mean values for organic matter content of the soils considered suggest that the 1% limit is low. The mean organic matter content of Al horizons for my Mollisols was 4.8%, ranging down to 2.4% for the Entisols. The mean of the Entisols was significantly greater than 1% (Student T test interpreted at the 95% confidence level, Zar 1974). This criterion from *Soil Taxonomy* should be reconsidered for forest and rangeland soils of the Intermountain Region of the United States.

Range Production Potentials

A knowledge of organic matter content in the mollic epipedon is effective in assessing potential range production. From 100 to 500 years are needed to achieve the equilibrium content of organic matter in the mollic epipedon (USDA 1975). Vegetative production of intermountain ranges shows considerable yearly variability, making it rather difficult to assign potentials based on a single year's production. Soil organic matter offers an alternative for assessing potential, since it is an indicator of production over a long period of time.

Organic matter content of Mollisols Al horizon showed a positive correlation with vegetative production (Table 7). The correlation ($r = .62$) would probably be improved if more quantitative vegetative sampling techniques than were used in this study were employed. Production showed a good relationship to both mollic epipedon depth and elevation on selected range sites. The following multiple regression equation was developed to assist in making estimates of production potentials on the Caribou National Forest. Production (kg/ha/yr) = –3053.8 + 54.0 (mollic epipedon depth, cm) + 1.57 (elevation, m); $n = 23$ ($r^2 = .82$).

Potassium-Magnesium Ratio Implications

Vegetative manipulation practices are common in forested lands of this region of the United States, with efforts being made to change the proportion of grasses, forbs, and shrubs in the pretreatment cover. A knowledge of the K-Mg ratio of the soil's Al horizon may be useful to the land manager in making better cost-effective proposals for

Table 5. Interpretative table for nutrient levels of the Al horizon by soil order.

Soil order	Level	P(ppm)	Ca(ppm)	K(ppm)	Mg(ppm)	Organic matter (%)
Mollisols	Low	<22	3	2	5	3.5
	Moderate	22 to 41	3 to 19	2 to 14	5 to 14	3.5 to 4.9
	High	42 to 61	20 to 35	15 to 28	15 to 24	5.0 to 6.0
	Very high	>61	35	28	24	6.0
Alfisols	Low	<38	2	3	6	1.6
	Moderate	38 to 53	2 to 13	3 to 14	6 to 10	1.6 to 3.2
	High	54 to 69	14 to 24	15 to 26	11 to 15	3.3 to 4.8
	Very high	>69	24	26	15	4.8
Entisols	Low	< 1	4	1	2	1.3
	Moderate	1 to 21	4 to 14	1 to 6	2 to 9	1.3 to 2.5
	High	21 to 42	15 to 25	7 to 12	10 to 16	2.6 to 3.5
	Very high	>42	25	12	16	3.5

TABLE 6. Horizon differences in phosphorus and magnesium contents by soil order.

	P(ppm)			Mg(ppm)		
Soil order	Al horizon	Subsoil horizon	Difference (%)	Al horizon	Subsoil horizon	Difference (%)
Mollisols	$\bar{x}$ = 39.0	21.8	79°	15.3	7.2	113°
	s = 20.0	20.2		9.2	2.1	
	n = 70					
Alfisols	$\bar{x}$ = 51.3	35.7	44	11.1	6.0	85°
	s = 17.4	24.7		5.2	1.4	
	n = 17					
Entisols	$\bar{x}$ = 23.8	20.2	18	11.4	10.9	5
	s = 23.6	19.0		11.3	9.7	
	n = 9					

°Indicates that the Al and subsoil horizon population values are significantly different ($P<0.05$) by use of the Wilcoxon paired sample test

range improvement expenditures (K. T. Harper, pers. comm.).

Table 8 shows the relationship of this ratio to the vegetative composition of the Mollisols. A significant negative correlation was found between the K-Mg ratio and grass composition of the sites. The composition of shrubs showed a significant positive correlation to the ratio, yet the coefficient of determination was low. Errors in the determination of shrub composition probably contributed to this fact. Woodward (1981) found the same general relationships as those presented in Table 8 for 30 species of Utah range plants. The root cation exchange capacity (CEC) for the species of his study averaged 33.5 meq/100g for the shrubs, 33.2 meq/100g for the forbs, and 14.7 meq/100g for the grasses. These differences affect nutrient uptake by the plants.

The strength of attraction of a cation to a negatively charged surface, i.e., plant root, is directly proportional to the charge on the surface and the cation, and inversely proportional to the distance between them (Russel 1973). It can be assumed that the higher the CEC of a root, the more the root would tend to attract Mg rather than K. Since the shrubs of this study had significantly higher root CEC values than the grasses, we would expect them to absorb Mg from the soil solution at a greater rate than the grasses. Conversely, the rate at which shrubs absorb K would be less than that for the grasses, since the shrub exchange sites are selectively attracting divalent cations, thus creating a soil solution around the root that is enriched in divalents and impoverished in respect to monovalent cations. These relations suggest that range sites with high K-Mg ratios in the soil would favor the growth of shrubs and sites with low K-Mg ratios would favor grass production (K. T. Harper, pers. comm.). This has indeed been the case for the Utah range plants studied by Woodward (1981) and the range sites of this study.

CONCLUDING REMARKS

This study of edaphic factors on selected forest and rangelands in southeastern Idaho

TABLE 7. The relationship of vegetative dry weight production to organic matter in the Mollisol soil order. Vegetative production (kg/ha/yr) = 172.9 + 259.1 (organic matter (%) in the Al horizon): r^2 = .38, n = 147

Organic matter (%) in Al horizon	Corresponding vegetative production predictions
1	431
2	691
3	950
4	1208
5	1468
6	1727
7	1986

NOTE: Regression slope is significantly different than 0 at a 95% confidence level.

TABLE 8. The relationship of the potassium magnesium ratio of the Al horizon to vegetative composition in the Mollisol soil order.

	K/Mg	Shrub (%)	Grass (%)
Mean	1.42	39.2	33.6
Standard deviation	1.05	19.6	15.4
Sample size	73	73	73

Grass (%) = $56.4\ e^{-.39\,(K/Mg)}$; r^2 = .60, n = 73
Shrub (%) = $27.8\ e^{.24\,(K/Mg)}$; r^2 = .18, n = 73

NOTE: 1. The exponential regressions provided gave better fits than did linear regressions.
2. Regression slopes are significantly different than 0 at a 95% confidence level.

provides relationships that will be of use to managers of wildlands in the Intermountain Region of the United States. More research on wildland soils of this region is needed, since large data bases are required for development of interpretive models of soil-plant relationships.

LITERATURE CITED

Baily, R. G. 1980. Description of the ecoregions of the United States. Misc. Pub. No. 1391. USDA Forest Service, Washington, D.C. 77 pp.

Black, C. A. 1965. Methods of soil analysis. Agronomy Series No. 9. American Society of Agronomy. Madison, Wisconsin. 1572 pp.

Brady, N. C. 1974. The nature and properties of soils. MacMillan Pub. Co., New York. 621 pp.

Fenneman, N. M. 1931. Physiography of western United States. McGraw-Hill Pub. Co., New York. 534 pp.

Jenny, H. 1961. Derivation of state factor equations of soil and ecosystems. Soil Sci. Soc. Amer. Proc. 25:385–388.

Russel, E. W. 1973. Soil conditions and plant growth. Longman Pub. Co., London. 810 pp.

USDA, Forest Service. 1969. Range environmental analysis handbook. USDA Forest Service, Intermountain Region, Ogden, Utah.

USDA, Soil Conservation Service. 1975. Soil taxonomy. Agricultural Handbook No. 436. U.S. Government Printing Office, Washington, D.C. 743 pp.

Wertz, W. A., and J. F. Arnold. 1972. Land systems inventory. USDA Forest Service, Intermountain Region. Ogden, Utah. 12 pp.

Woodward, R. A. 1981. An ecological consideration of the significance of cation exchange capacity of roots of some Utah range plants. Unpublished thesis. Brigham Young University, Provo, Utah. 29 pp.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, New Jersey. 600 pp.

BREEDING BIRDS OF AN ANCIENT BRISTLECONE PINE STAND IN EAST CENTRAL NEVADA

Dean E. Medin[1]

Abstract.— This paper describes features of the breeding bird population of a Great Basin ancient bristlecone pine stand on Wheeler Peak in White Pine County, east central Nevada. The bird population was determined by spot-mapping methods on a 20-ha plot during June and July 1981. The density of breeding birds was 82 pairs per 40 ha. Fourteen species were territorial. The most abundant species were the Dark-eyed Junco, Mountain Chickadee, Mountain Bluebird, and Townsend's Solitaire. Other common breeding species included the Cassin's Finch, Yellow-rumped Warbler, Pine Siskin, and Dusky Flycatcher. There were 410 individual breeding birds per km^2. When expressed as standing crop biomass, the Townsend's Solitaire was the predominant species, followed by the Dark-eyed Junco, American Robin, Mountain Bluebird, and Northern Flicker. Total standing crop biomass was 95 g/ha. None of the breeding birds were restricted to the bristlecone pine stand. The structure of the breeding bird community in the bristlecone pine forest compared best to those of the Rocky Mountain and Northern Boreal forest regions.

Bristlecone pine (*Pinus longaeva*), the oldest living tree of verified age presently known, grows on dry, rocky subalpine habitats in the Great Basin. Scattered stands occur in the Utah Plateaus, west through Nevada to the White, Inyo, and Panamint mountains of eastern California (Cronquist et al. 1972). The bristlecone pine is a gnarled and bushy tree, often exceeding 15 m in height and with a thick, shallowly lobed trunk. It grows at high elevations, sometimes with limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*).

The longevity and esthetic appeal of the sculptured bristlecone pine trees and their environments have generated interest among scientists and recreationists (Ferguson 1968). Trees over 3,000 years old are common, and several over 4,000 years have been found (Currey 1965). In 1959 the USDA Forest Service designated 11,330 ha of the Humboldt National Forest in the Snake Range of eastern Nevada as the Wheeler Peak Scenic Area in recognition of the exceptional scenic, botanical, and geologic attractions of the area and to provide protection for the ancient bristlecone pine stands on Wheeler Peak and nearby Mount Washington.

The avifauna of these unique stands of ancient trees have received little quantitative study. This paper describes features of the breeding bird population of a stand of bristlecone pine on Wheeler Peak in White Pine County, east central Nevada.

Study Area and Methods

The bristlecone pine stand is at the mouth of a deep glacial cirque on the northeast face of Wheeler Peak (elevation 3,981 m), 62 km southeast of Ely, Nevada. The stand covers about 55 ha and ranges in elevation from about 3,100 m to the upper limits of tree growth near 3,300 m. The slopes are steep and covered with coarse-textured glacial till composed of quartzite blocks (Currey 1965). The area has a dry, cool climate with maximum precipitation occurring in late winter and spring. Mean annual precipitation is about 76 cm (Beasley and Klemmedson 1980).

Bristlecone pine dominates the stand, making up 54% of the total tree composition; limber pine (34%) and Engelmann spruce (12%) are the primary associates (Beasley and Klemmedson 1976). Total basal area ranges from about 19 m^2/ha on harsh sites to 43 m^2/ha on favorable sites (Table 1). At its lower elevational limits, the stand grades into the mixed-conifer forest of Engelmann spruce, limber pine, and Douglas-fir (*Pseudotsuga menziesii*) typical of the Snake

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Range. The understory vegetation is generally sparse. Common shrubs include gooseberry (*Ribes montigenum*), raspberry (*Rubus idaeus*), common juniper (*Juniperus communis*), and goldenweed (*Haplopappus macronema*).

A 20-ha plot was censused for breeding birds using the Williams spot-map method (International Bird Census Committee 1970). Methodological difficulties and other specific problems of the mapping technique are summarized by Oelke (1981) and Dawson (1981). The census plot was chosen to best represent the stand of bristlecone pine. The upper boundary approached timberline, and a shallow, rocky morainal pond (about 0.8 ha) was included near the lower margin of the plot. The square plot was surveyed and gridded in a Cartesian coordinate system with points flagged and numbered with stakes at 75-m intervals. Ten census visits were made to the plot from 18 June to 17 July 1981. Most of the work was done from sunrise to late morning when birds were most active. To ensure complete coverage, the plot was censused by walking within 50 m of all points on the grid. Observations extended well beyond plot boundaries.

At the end of the sampling period, concentrated groups of observations were circled as indicating areas of activity or approximate territories. Fractional parts of boundary territories were recognized. Results were converted to the number of pairs of breeding birds per 40 ha. Shannon's formula ($H' = -\Sigma p_i \ln p_i$, where $p_i = N_i/N$ is the proportion of the collection belonging to the *i*th species) was used to calculate the species diversity index (Shannon and Weaver 1963).

RESULTS AND DISCUSSION

The density of breeding birds occupying the bristlecone pine census plot was 82 pairs per 40 ha (Table 2). Fourteen species were territorial. The most numerous species, each making up more than 10% of the population and collectively accounting for 53%, were the Dark-eyed Junco, Mountain Chickadee, Mountain Bluebird, and Townsend's Solitaire. Other common species, each including 5% to 10% of the population, were the Cassin's Finch, Yellow-rumped Warbler, Pine Siskin, and Dusky Flycatcher. There were 410 individual breeding birds per km^2. When expressed as standing crop biomass, the Townsend's Solitaire was the predominant species, followed by the Dark-eyed Junco, American Robin, Mountain Bluebird, and Northern Flicker. Those five species made up 65% of the standing crop biomass of the breeding avifauna. Total standing crop biomass was 95 g/ha.

In addition to the 14 territorial species listed in Table 2, the Common Raven (*Corvus corax*), Clark's Nutcracker (*Nucifraga columbiana*), and Rosy Finch (*Leucosticte arctoa*) were commonly observed. Rocky cliffs and talus slopes adjacent to the census plot provided nesting substrates for the Raven and Rosy Finch. The Golden Eagle (*Aquila chrysaetos*), Violet-green Swallow (*Tachycineta thalassina*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), and Red Crossbill (*Loxia curvirostra*) were infrequent visitors.

Species may be categorized by foraging substrate (air, foliage, timber, or ground) and dietary habits (insectivore, omnivore, or granivore). Categories indicated in Table 2

TABLE 1. Characteristics of Wheeler Peak bristlecone pine stand on 6 sites.[a]

Relative site quality	Understory plant cover (%)	Stone cover (%)	Basal area: Bristlecone pine (m^2/ha)	Basal area: Engelmann spruce (m^2/ha)	Basal area: Limber pine (m^2/ha)	Basal area: Total (m^2/ha)	Mean area per tree (m^2)
Favorable	8.80	57.3	15.6	15.8	7.1	38.5	30.0
	3.45	59.7	6.9	18.6	9.6	35.1	24.5
	1.94	45.4	7.8	18.4	17.2	43.4	22.0
Harsh	3.08	83.6	13.5	7.3	1.6	22.4	36.5
	3.01	71.5	16.3	7.1	2.8	26.2	46.0
	0.79	89.8	17.0	1.8	0.7	19.5	135.0

[a] From Beasley and Klemmedson (1980).

are based upon those developed by Salt (1953) as modified by Diem and Zeveloff (1980). The 14 breeding bird species were distributed over eight different foraging categories. Foliage gleaners and ground feeders were equally divided among the species represented, and those forms made up the largest proportion of all foraging categories. Among the foliage feeders, insectivorous species predominated. Ground-gleaning forms were also mainly insectivorous. Three species were largely granivorous. The aerial-sally category was represented by only one species (Dusky Flycatcher), as was the timber-gleaning category (White-breasted Nuthatch). Timber-drilling forms were conspicuous by their absence in the bristlecone pine stand. Wiens (1978) showed that foliage-feeding forms numerically dominate the avifauna in North American coniferous forests, with ground-feeding, timber-foraging, and aerial feeders less important, in decreasing order. The avifauna of the bristlecone pine forest appear to generally fit this pattern.

The substrates used for nesting provide additional information about the bird population. Of the 14 breeding bird species, 7 (50%) nest in foliage, 4 (29%) use cavities, and

TABLE 2. Ecological attributes and population density of the breeding birds of an ancient bristlecone pine stand, Wheeler Peak, Nevada, June–July 1981.

Species	Species weight[a] (g)	Nesting substrate[b]	Foraging category[c]	Population density (pairs/40 ha)
Broad-tailed Hummingbird (*Selasphorus platycercus*)	3.5	F	FNI	4.0
Northern Flicker (*Colaptes auratus*)	134.1	C	GGI	1.5
Dusky Flycatcher (*Empidonax oberholseri*)	12.4	F	ASI	5.5
Mountain Chickadee (*Parus gambeli*)	11.3	C	FGI	11.5
White-breasted Nuthatch (*Sitta carolinensis*)	17.4	C	TGO	1.0
Rock Wren (*Salpinctes obsoletus*)	15.9	G	GGI	0.5
American Robin (*Turdus migratorius*)	69.9	F	GGI	3.5
Hermit Thrush (*Catharus guttatus*)	29.8	F	FFO	2.5
Mountain Bluebird (*Sialia currucoides*)	26.6	C	GGI	9.0
Townsend's Solitaire (*Myadestes townsendi*)	32.9	G	FFO	8.5
Yellow-rumped Warbler (*Dendroica coronata*)	13.0	F	FGI	6.5
Cassin's Finch (*Carpodacus cassinii*)	26.6	F	GGG	7.5
Pine Siskin (*Carduelis pinus*)	11.6	F	FGG	6.0
Dark-eyed Junco (*Junco hyemalis*)	18.1	G	GGG	14.5

TOTAL NUMBER OF SPECIES = 14
TOTAL PAIRS PER 40 HA = 82
TOTAL INDIVIDUALS PER KM^2 = 410

STANDING CROP BIOMASS = 95 G/HA
SPECIES DIVERSITY INDEX = 2.39
PLOT SIZE = 20 HA

[a] Species weights from Linsdale (1936), Behle (1943), Salt (1957), and Johnson (1965).

[b] F = foliage, C = cavity, G = ground.

[c] FNI = foliage nectivore–insectivore, GGI = ground-gleaning insectivore, ASI = aerial sally-feeding insectivore, FGI = foliage-gleaning insectivore, TGO = timber-gleaning omnivore, FFO = foliage-feeding omnivore, FGG = foliage-gleaning granivore, GGG = ground-gleaning granivore.

TABLE 3. Features of breeding bird community structure in coniferous forests of different regions of North America.[a]

		Number of species		Density (individuals/km^2)		Standing crop biomass (g/ha)	
Region	Censuses	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Northwest	17	15.4	6.1	1456	621	283	102
Sierra Nevada	6	21.3	5.0	796	410	251	215
Great Basin[b]	1	14.0	–	410	–	95	–
Rocky Mountain	17	14.0	5.0	736	575	188	147
Northern Boreal	4	14.5	3.9	466	216	80	32
Southeast	10	21.6	5.5	1221	407	281	95
Northeast (mature)	18	22.6	4.2	1341	343	273	146
Northeast (immature)	9	11.1	3.7	329	150	65	50

[a] From Wiens (1978).
[b] Data from this study included to facilitate comparisons.

3 (21%) nest on the ground (Table 2). Numerically, foliage nesters made up 43% of the population; ground nesters and cavity nesters each accounted for about 28% of the breeding avifauna of the bristlecone pine stand. The Northern Flicker is the only primary hole-nesting species represented. Secondary cavity nesters (Mountain Chickadee, Mountain Bluebird, White-breasted Nuthatch) made up the bulk of the hole-nesting forms. The Dark-eyed Junco was predominate among the ground nesters.

None of the breeding birds listed in Table 2 are restricted to the bristlecone pine forest. With the exception of the Common Raven, all the birds observed in the Wheeler Peak bristlecone pine stand are included among the 80 species designated as boreal by Behle (1978) in his study of the avifauna of 14 boreal islands in western and southeastern Utah. Also, 11 of the 14 birds that Johnson (1975) called "standard" boreal species of Great Basin montane island avifaunas are represented in the bristlecone pine forest. Johnson considered this standard group of interest ecologically because the species that comprise it nearly always occur together and may be taken to represent the basic community of western American boreal birds.

Wiens (1978) summarized the structure of breeding bird communities in the coniferous forests of different regions of North America (Table 3). In comparison, the number of breeding bird species encountered in the Wheeler Peak bristlecone pine stand is lower than the average number in coniferous forests of the northwestern, northeastern, and southeastern regions and in the Sierra Nevada. The species total in the bristlecone pine stand is similar to the average number of breeding species recorded in the Rocky Mountain region and the Northern Boreal forest of northwestern Canada and southeastern Alaska. The number of birds per unit area and the standing crop biomass of breeding birds in the bristlecone pine forest compare most favorably with those of the Northern Boreal forest region. Johnson (1975) commented on the seeming paucity of both total species numbers and numbers of individuals of a given species on many montane islands of the Great Basin when compared with areas of similar size in the Sierra Nevada or the Rocky Mountains. The quantitative avifaunal data from the Wheeler Peak stand of bristlecone pine tend to verify this impression.

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LITERATURE CITED

BEASLEY, R. S., AND J. O. KLEMMEDSON. 1976. Water stress in bristlecone pine and associated plants. Commun. in Soil Science and Plant Analysis 7:609–618.

______. 1980. Ecological relationships of bristlecone pine. Amer. Midl. Nat. 104:242–252.

BEHLE, W. H. 1943. Birds of Pine Valley Mountain Region, southwestern Utah. Univ. Utah, Biol. Series 7:1–85.

______. 1978. Avian biogeography of the Great Basin and Intermountain Region. Pages 55–80 *in* Intermountain biogeography: a symposium. Great Basin Nat. Memoirs No. 2, Brigham Young Univ., Provo, Utah.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora. Vol. 1. Hafner Publ. Co., New York. 270 pp.

CURREY, D. R. 1965. An ancient bristlecone pine stand in eastern Nevada. Ecology 46:564–566.

DAWSON, D. G. 1981. The usefulness of absolute ("census") and relative ("sampling" or "index") measures of abundance. Pages 554–558 *in* C. J. Ralph and J. M. Scott, eds., Estimating numbers of terrestrial birds. Cooper Ornithol. Soc., Stud. Avian Biol. 6.

DIEM, K. L., AND S. I. ZEVELOFF. 1980. Ponderosa pine bird communities. Pages 170–197 *in* Workshop Proc. Management of western forests and grasslands for nongame birds. USDA For. Serv. Gen. Tech. Rep. INT-86. Intermountain Forest and Range Experiment Station, Ogden, Utah.

FERGUSON, C. W. 1968. Bristlecone pine: science and esthetics. Science 159:839–846.

INTERNATIONAL BIRD CENSUS COMMITTEE. 1970. An international standard for a mapping method in bird census work. Audubon Field Notes 24:722–726.

JOHNSON, N. K. 1965. The breeding avifaunas of the Sheep and Spring ranges in southern Nevada. Condor 67:93–124.

______. 1975. Controls of number of bird species on montane islands in the Great Basin. Evolution 29:545–567.

LINSDALE, J. M. 1936. The birds of Nevada. Pac. Coast Avifauna No. 23:1–145.

OELKE, H. 1981. Limitations of the mapping method. Pages 114–118 *in* C. J. Ralph and J. M. Scott, eds., Estimating numbers of terrestrial birds. Cooper Ornithol. Soc., Stud. Avian Biol. 6.

SALT, G. W. 1953. An ecologic analysis of three California avifaunas. Condor 55:258–273.

______. 1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. Condor 59:373–393.

SHANNON, C. E., AND W. WEAVER. 1963. The mathematical theory of communication. Univ. of Illinois Press, Urbana, Illinois. 117 pp.

WIENS, J. A. 1978. Nongame bird communities in northwestern coniferous forests. Pages 19–31 *in* Workshop Proc. Nongame bird habitat management in the coniferous forests of the western United States. USDA For. Serv. Gen. Tech. Rep. PNW-64. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

CHECKLIST OF VASCULAR PLANTS OF THE CANYON AND CHURCH MOUNTAINS

Sherel Goodrich[1]

Abstract. A checklist of vascular plants of the Canyon and Church mountains, Juab and Millard counties, Utah, is provided. Frequency, distribution, and flowering time of taxa within the study area are indicated. Collection numbers of voucher specimens are listed. Physiography, climate, and plant communities of the area are briefly described.

People involved in rangeland and forest inventories studies are frequently faced with the need to identify plants. Plant checklists for rather small areas can be very helpful to these people or anyone who would like to know the name of a plant. Local checklists greatly reduce the number of choices possible in comparison to the numerous choices from manuals covering large areas. In the absence of completed floristic treatments for the Intermountain Region, localized checklists are often the main source of information about the flora of an area. In addition, phytogeography is of great interest to ecologists and others. Checklists of specific mountain ranges provide a basis for many phytogeographic studies. The primary objective of this study is to provide a plant list for the use of those working in the Canyon Mountains area. Some other local checklists of the Intermountain area have been authored by Graham 1937, Harris 1980, Lewis 1970, 1971, 1973, Linsdale et al. 1952, MacMillian 1948, Neese 1981, Preece 1950, and Welsh 1957.

Work is currently under way on three major floras (*Intermountain Flora, The Atlas of Vascular Plants of Utah, and Utah Flora*[2]) that include the area of this study. These treatments are dependent upon plant specimens for descriptions and distribution data of plant taxa. The secondary objective of this study was to provide specimens for these projects. Many specimens collected during this study are deposited at New York Botanical Garden, University of Utah, Utah State University, and Brigham Young University, at which institutions the above floras are being written.

Study Area

The area included in this study is within the Canyon and Church Mountains in Millard and Juab counties, Utah (Fig. 1). These mountains are at the eastern edge of the Great Basin. The Canyon Mountains are a narrow, steep, fault-block range that is about 32 km (20 miles) long with a north-south axis. Elevation varies from about 1463 m (4800 ft) to 2962 m (9717 ft) at the top of Fool Peak. Much of the range is steep and rocky with massive rock outcrops forming cliffs and ledges mainly of precambrian quartzite and with some limestone. The Church Mountains are at the south end of Canyon Mountains and consist of a few low hills with an east-west axis. The boundary of the Fishlake National Forest encompasses the two ranges, and the National Forest Boundary was used as a boundary for this study.

The climate is typically that of the Great Basin, with cold moist winters and warm dry summers. Two weather stations (Oak City and Scipio) with long-term records are adjacent to the area. Average annual precipitation was 30.63 cm (12.06 inches) for 65

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[2] These floras are in various stages of completion. Two of the six volumes of the *Intermountain Flora* are published (Cronquist et al. 1972, 1977). *The Atlas of Vascular Plants of Utah* is in preparation. Several plant families of the *Utah Flora* have been published separately or a few together (Welsh 1978, 1980, 1982, Welsh and Reveal 1977).

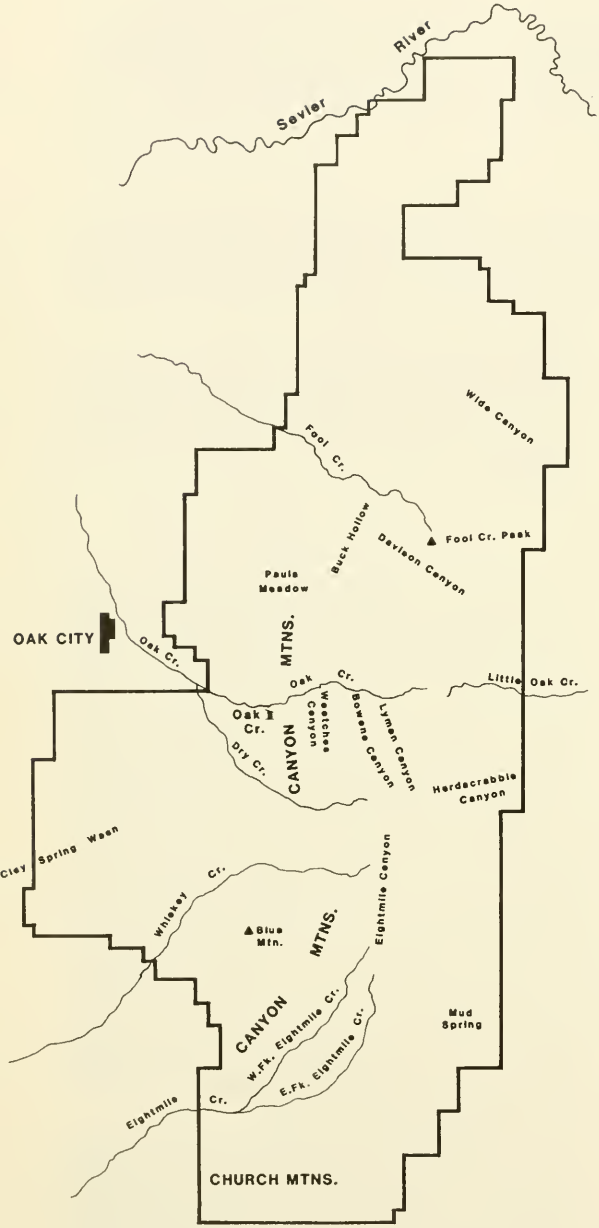
Sevier
River
Wide Canyon
Fool Cr.
Buck Hollow
Devilson Canyon
▲ Fool Cr. Peak
Pauls Meadow
MTNS.
OAK CITY
Oak Cr.
Oak Cr.
Little Oak Cr.
Oak Cr.
Weetches Canyon
Bowens Canyon
Lyman Canyon
Dry Cr.
CANYON
Hardscrabble Canyon
Clay Spring Wash
Whiskey Cr.
▲Blue Mtn.
MTNS.
Eightmile Canyon
Mud Spring
CANYON
W.Fk. Eightmile Cr.
E.Fk. Eightmile Cr.
Eightmile Cr.
CHURCH MTNS.

Fig. 1 Checklist collection area.

years at Oak City, and 31.34 cm (12.34 inches) for 76 years at Scipio. Figure 2 shows the monthly distribution of precipitation at these two stations.

The average frost-free period was 144 days at Oak City for 1956 through 1979. Scipio is in a basin where cold air drainage is common, and this station has a considerably shorter frost-free period. The average frostfree period was 103 days for 1956 to 1979, or 41 days shorter than at Oak City. At Oak City, 12 May was the average day for the last freezing temperature in the spring for 1956 to 1979. This date at Scipio was 2 June, for the same period, or about 20 days later than at Oak City. Figure 3 shows the average monthly temperature for the two stations.

Most of the lower elevations in the study area are out of the zone of cold-air drainage in which Scipio is located, and the climate of the area is probably more nearly like that at Oak City. The upper elevations likely have considerably more precipitation and colder temperatures.

PLANT COMMUNITIES

Pinyon-juniper

Pinyon pine (*Pinus edulis*), singleleaf pinyon (*P. monophylla*), and juniper (*Juniperus osteosperma*) communities cover the Church Mountains and lower hills of the Canyon Mountains. They extend up to near the high points of the Canyon Mountains on south exposures before being replaced by mountain brush communities. On north exposures, they are replaced at much lower elevations. Juniper dominates, and the pinyons are nearly lacking at lower elevations, but at upper elevations the pinyons are most abundant. The limits of pinyon and juniper seem controlled by cold temperatures of low-level inversions in the valleys and by increasing cold temperatures with increasing elevation. The lower limits are likely also influenced by lower precipitation. Reference to the pinyon-juniper zone is frequently made in the text. This refers somewhat loosely to that elevational range at which either or both pinyon and juniper are common. This varies, roughly, at the lower limit from 1585 to 1707 m (5200–5600 ft) to an upper limit of about 2438 m (8000 ft) on south exposures, and up to only about 1830 m (6000 ft) on north exposures.

Mountain Brush

Mountain brush communities border the upper edge of pinyon-juniper communities and follow canyons and drainages well down into the pinyon-juniper zone. They are dominated by one or more of the following plants: Oak (*Quercus gambelii*), curlleaf mountain mahogany (*Cercocarpus ledifolius*), true mountain mahogany (*C. montanus*), greenleaf manzanita (*Arctostaphylos patula*), and chokecherry (*Prunus virginiana*). Oak and curlleaf mountain mohagany are by far the most abundant of these plants. Communities dominated by curlleaf mountain mahogany are typically found on shallow rocky soils and often on warm exposures, while those dominated by oak are on somewhat more favorable soils and sometimes on cooler exposures. Along canyon bottoms, oak often becomes tree like, and it is sometimes associated with bigtooth maple (*Acer grandidentatum*). As referred to in the text, the mountain brush zone is that area typically above the pinyon-juniper zone where any of the above-listed plants are dominant.

Sagebrush

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities cover extensive areas just beyond the boundary of this study area, such as in Little Valley on the east side of the Canyon Mountains, where most of this sagebrush was removed in an extensive burn in 1981. Soils of these communities often have a hardpan that is high in carbonates. This pan typically occurs from 30 to 55 cm (12 to 22 inches) below the surface. Much of the area covered by Wyoming big sagebrush is below the pinyon-juniper zone. An abundance of this sagebrush over a large area probably indicates that average annual precipitation is between 20.32 and 25.40 cm (8–10 inches).

Vasey sagebrush (*A. tridentata* ssp. *vaseyana*) becomes abundant at about the lower edge of the pinyon-juniper zone and extends to the highest elevations of the area. With juniper, it covers extensive areas at the lower elevations of the pinyon-juniper zone where, it is most common on concave topography. On convex topography, where soils are more shallow, it is replaced by black sagebrush (*A. nova*). Vasey sagebrush forms communities with mountain brush species and with low sagebrush (*A. arbuscula*) on slopes and in canyons over much of the middle and upper elevations of the area. Vasey sagebrush–grass communities are quite limited. They are mostly at the upper elevations in small areas of concave topography.

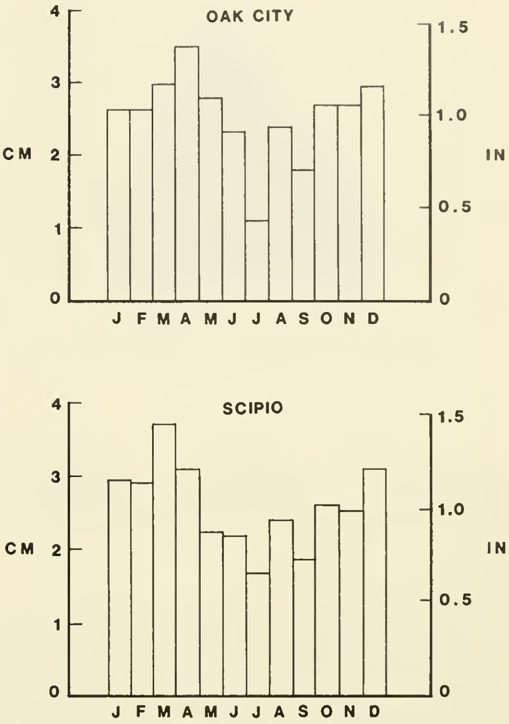

Fig. 2 Average monthly precipitation at Oak City and Scipio.

Black sagebrush forms communities on convex topography with juniper, cliffrose (*Cowania mexicana*), and bluebunch wheatgrass (*Agropyron spicatum*) within the pinyon-juniper zone. Occasionally it is common up in the mountain brush zone, but in this zone it is usually restricted to limestone.

Basin big sagebrush (*A. tridentata* ssp. *tridentata*) communities are restricted mostly to deep alluvial soils along drainages at the lower elevations of the area.

Low sagebrush forms communities of considerable size with various xeric grasses and forbs on convex, windswept slopes and ridges in and above the pinyon-juniper zone.

Aspen

Aspen (*Populus tremuloides*) is quite limited in the Canyon mountains, and the stands

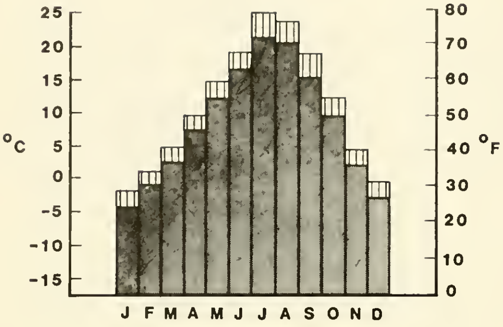

Fig. 3 Average monthly temperature at Oak City (lined) and Scipio (shaded).

are usually rather small. These communities are usually found along drainages and on concave slopes, and often on cool exposures.

Fir

White fir (*Abies concolor*), sometimes in association with Douglas-fir (*Pseudotsuga menziesii*) forms closed communities on cool exposures at upper elevations of the Canyon Mountains.

PLANTS OF UNIQUE HABITATS

Plants of Aeolian Sand

The following plants were found to be restricted, or nearly restricted, to wind-deposited sand: *Abronia elliptica, Ambrosia acanthicarpa, Amsinkia intermedia, Astragalus ceramicus, Chrysothamnus nauseosus* ssp. *turbinatus, Cryptantha circumscissa, C. confertiflora, Cymopterus fendleri, Eriogonum kearney, Grayia spinosa, Lupinus brevicaulis, Nama densum, Oenothera pallida, Penstemon angustifolia, Prenanthella exigua, Psoralea lanceolata, Rhus trilobata, Streptanthella longirosteris, Townsendia florifera,* and *Triterocalyx micranthus.*

Plants of Rocky Places

Much of the mid and upper elevations of the Canyon Mountains is composed of massive rock outcrops. The outcrops provide habitat for several specialized plants that grow mostly in rock crevices or on rock faces. Among these specialized plants are: *Cystopteris fragilis, Cryptantha compacta, Epilobium canum, Erigeron nauseosus, Geranium parryi, Haplopappus watsonii, Heterotheca villosa, Heuchera rubescens, Lepidium montanum* var. *heterophyllum, Macheranthera kingii* var. *barnebyi, Pellaea breweri, Petrophytum caepitosum, Polystichum scopulinum, Sedum debile, Selaginella watsonii, Sphaeromeria diversifolia, Solidago sparsiflora,* and *Trifolium andinum.* Other plants that occur mostly in rocky places are: *Allium brandegii, Echinocereus triglochidiatus, Epilobium nevadense, Eriogonum brevicaule, Petradoria pumila, Potentilla glandulosa, Silene douglasii,* and *Xanthocephalum petradoria.*

Plants of Old Lake Deposits above the Sevier River

Lacustrine deposits of old Lake Bonneville above the Sevier River at the north edge of the area provide some of the most unusual habitat of the area. These deposits are saline, or alkaline and seleniferous in places. Several plants of salt-desert shrub regions enter the area on these deposits, including: *Atriplex confertifolia, A. falcata, Kochia americana ,Sarcobatus vermiculatus,* and *Thelypodium sagittatum.* Other plants on these deposits, and apparently nowhere else in the area, are: *Astragalus bisulcatus, A. calycosus, Hedysarum boreale, Hymenoxys cooperi, Penstemon confusus,* and *Stanley pinnata.*

NEW TAXA

Macheranthera kingii var. *barnebyi* and *Xanthocephalum petradoria* have been described from collections taken from the Canyon Mountains during this study. Collections referred to here as *Geranium parryi* may be worthy of varietal distinction, and those referred to as *Lesquerella occidentalis* will likely be described as something new (pers. comm. from Reed C. Rollins, Asa Gray professor emeritus of systermatic botany, Harvard University).

RANGE EXTENSION

Anemone tuberosa. Disjunct by about 150 km (93 mi) northeast from near the Desert Experimental Range in Beaver and Millard counties, and about 140 km (87 mi) south of a remarkable collection (B. Albee 2288) from Stansbury Island.

Cryptantha compacta. Previously known only from Western Millard County.

Cymopterus acaulis. Collections from just south of Oak City apparently represent the southernmost extent of the species in the Great Basin. These may represent a new variety.

Epilobium nevadense. Range extension of 230 km (143 mi) from Beaver Dam mountains of Washington County.

Penstemon leonardii. Range extention of 60 km (37 mi) from Mt. Nebo, Juab County.

Polystichum scopulinum. Third known location for Utah, previously reported for Salt Lake and Washington counties (Cronquist et al. 1972).

Trifolium andinum. Third known location for Utah, previously reported for north slope of the Uinta Mountains, Daggett County, and Navajo Mountain, Kane County (Welsh 1978), about 275 km (171 mi) from either of these locations.

The Checklist

The checklist is arranged alphabetically by family, genus, and species without regard for phylogenetic order. Nomenclature mostly follows that of Welsh et al. (1981). The list is primarily based on collections and observations that I made during 1980, 1981, and 1982. A very limited herbarium search was made to find a few expected taxa for which I had no records. Unless otherwise designated, the collections numbers are mine. Taxa for which no collection numbers are given were observed but not collected. The most complete set of specimens are deposited at Brigham Young University, Provo, Utah (BRY). Many other specimens were also deposited at: Intermountain Forest and Range Experiment Station, Shrub Sciences Laboratory, Provo, Utah (SSLP); New York Botanical Garden, New York, New York (NY); Region Four, Forest Service, Ogden, Utah (OGDF); Supervisors Office, Fishlake National Forest, Richfield, Utah; and at Garrett Herbarium, University of Utah, Salt Lake City, Utah (UT).

The Flora

A total of 65 families, 244 genera, 440 species, and 26 infraspecific taxa are listed. Of the species, 20% are in Asteraceae. Poaceae, Brassicaceae, Fabaceae, Rosaceae, and Scrophulariaceae each contain 10%, 8%, 6%, 5%, and 4% of the taxa, respectively. Chenopodiaceae, Polemoniaceae, Polygonaceae, and Ranunculaceae each contain about 3% of the species. Apiaceae, Cyperaceae, and Onagraceae each have about 2% and the remaining 52 families each have less than 2%.

Literature Cited

Cronquist, A., A. H. Holmgren, N. H. Holmgren, and J. L. Reveal. 1972. Intermountain flora. Vol. 1. Hafner Publishing Co. Inc., New York. 270 pp.

Cronquist, A., A. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1977. Intermountain flora. Vol. 6. Columbia Univ. Press, New York. 584 pp.

Graham, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. Ann. Carnegie Museum 26:1–432.

Harris, J. G. 1980. A vascular flora of the San Rafael Swell, Utah. Unpublished thesis, Brigham Young Univ., Provo, Utah. 173 pp.

Lewis, M. E. 1970. Alpine rangelands of the Uinta Mountains. USDA Forest Service. Mimeo. 75 pp.

———. 1971. Flora and major plant communities of the Ruby-East Humboldt Mountains. USDA Forest Service. Mimeo. 62 pp.

———. 1973. Wheeler Peak area species list. USDA Forest Service. Mimeo. 17 pp.

Linsdale, M. A., J. T. Howell, and J. M. Linsdale. 1952. Plants of the Toiyabe Mountains area, Nevada. Wasmann J. Biol. 10:129–200.

McMillan, C. 1948. A taxonomic and ecological study of the Deep Creek Mountains of central western Utah. Unpublished thesis. Univ. of Utah, Salt Lake City, Utah. 99 pp.

Neese, E. J. 1981. A vascular flora of the Henry Mountains, Utah. 370 pp.

Ptrrvr, S. J., Jr. 1950. Floristic and ecological features of the Raft River Mountains of Northwestern Utah. Unpublished thesis. Univ. of Utah, Salt Lake City, Utah. 86 pp.

Welsh, S. L. 1957. An ecological survey of the vegetation of the Dinosaur National Monument, Utah. Unpublished thesis. Brigham Young Univ. Provo, Utah. 86 pp.

———. 1978. Utah flora: Fabaceae (Leguminosae). Great Basin Nat. 38:225–367.

———. 1980. Utah Flora: Malvaceae. Great Basin Nat. 40:27–37.

———. 1980. Utah flora: Miscellaneous families. Great Basin Nat. 40:38–57.

———. 1982. Utah flora: Rosaceae. Great Basin Nat. 42:1–44.

Welsh, S. L., and J. L. Revel. 1977. Utah flora: Brassicaceaae (Cruciferae). Great Basin Nat. 37:279-364.

Welsh, S. L., N. D. Atwood, S. Goodrich, E. Neese, K. H. Thorne, and B. Albee. 1981. Preliminary index of Utah vascular plant names. Great Basin Nat. 41:1-108.

Species List

Aceraceae

***Acer glabrum* Torr.** Occasional on slopes, mostly within mountain brush and aspen communities. May-June. 14359, 16843.

***Acer grandidentatum* Nutt. in T. & G.** Occasional to locally common along major drainages. May-June. 10427, 15317, 17360; Welsh 16424.

Amaranthaceae

***Amaranthus albus* L.** Seen at the mouth of Oak Creek Canyon in a burnedover cottonwood-willow-oak community. June-October. 17320.

***Amaranthus graecizans* L.** Introduced from the Old World, adventive with disturbance, an early succession plant on chared ground where slash piles from pinyon-juniper chainings have been burned. June-July. 14111.

Anacardiaceae

***Rhus glabra* L.** Infrequent along ephemeral drainages of lower Eightmile Creek in the pinyon-juniper zone. June-July. 14114, 14239.

***Rhus trilobata* Nutt. in T. & G.** Locally common to abundant on aeolian sand in and below the pinyon-juniper zone, infrequent elsewhere. May-June. 13779, 14240.

Apiaceae

***Cymopterus acaulis* (Pursh) Raf.** Infrequent on aeolian sand along the west edge of the area in pinyon-juniper communities. April-May. 15279, 15311, 15313, 15404.

***Cymopterus purpurascens* (Gray) Jones.** Infrequent on sandy-clay deposits of old Lake Bonneville above the Sevier River at the extreme north limit of the area, rare in the pinyon-juniper zone elsewhere in the area. March-May. 13838, 13852, 15272; Welsh 16420.

***Lomatium dissectum* (Nutt.) Math. & Const. var. *catonii* (Coult. & Rose) Cronq.** Infrequent in oak and oak-maple-white fir communities. May-June. 14199, 15324, 15605.

***Lomatium foeniculaceum* (Nutt.) Coult. & Rose var. *macdougalii* (Coult. & Rose) Cronq.** Occasional to common in sagebrush-juniper, and low sagebrush communities. May-June. 13781, 13847, 13894, 13902, 13909, 13932, 13933, 15378; Welsh 14605.

***Lomatium grayi* Coult. & Rose.** Occasional to common in pinyon-juniper, sagebrush, and mountain brush communities, mostly on quartzite, but also on limestone. May-June. 13976, 14020, 14365, 15287, 15325, 15391, 15553, 15559; Foster 6538; Welsh 16397, 16410, 16598. Some plants of the Canyon Mountains are transitional from var. *grayi* to var. *depauperatum* (Jones) Mathias.

***Lomatium macrocarpum* (H. & A.) Coult. & Rose.** Infrequent to occasional in sagebrush-juniper, pinyon-juniper, and mountain brush communities. April-June. 14082, 14208, 15286, 15550, 15632.

***Orogenia linearifolia* Wats.** Infrequent to locally common in various plant communities above the pinyon-juniper zone. May-June (July at the edge of melting snow banks). 14354A, 15394; Welsh 16432.

***Osmorhiza chilensis* H. & A.** Occasional to locally common in aspen, fir, and oak-maple communities on canyon bottons. May-June. 14326, 15586.

***Osmorhiza occidentalis* (Nutt.) Torr.** Locally common in mesic mountain brush and aspen communities. June-July. 14314, 15800.

Apocynaceae

***Apocynum androsaemifolium* L.** Locally common in Oak Creek Canyon, apparently rather rare elsewhere, mountain brush communities. July-August. 15791, 17312; Foster 6552.

Asclepiadaceae

***Asclepias asperula* (Dcne.) Woodson.** Infrequent in sagebrush and pinyon-juniper communities. June-July. 14282.

***Asclepias speciosa* Torr.** Seen at a single location in a chainedover pinyon-juniper woodland between Church and Canyon mountains. June-July. 14133.

Asteraceae

***Achillea millefolium* L.** Occasional in various plant communities over a wide elevational range. June-September. 14297; Foster 6534.

***Agoseris aurantiaca* (Hook.) Greene.** Seen only at East Fork Eightmile Canyon, with oak and sagebrush. June. 14010.

***Agoseris glauca* (Pursh) Raf.** Common in several plant communities over a wide elevational range. May-June. 13792, 13803, 13928.

***Ambrosia acanthicarpa* Hook.** Locally common to abundant on sandy ground, mostly in and below the pinyon-juniper zone. August-September. 16391.

***Antennaria dimorpha* (Nutt.) T. & G.** Occasional to locally common in pinyon-juniper and sagebrush communities. Late April-June. 13768A, 13786, 15380.

***Antennaria microphylla* Rydb.** Occasional and locally common in various plant communities. May-July. 14005.

***Antennaria parvifolia* Nutt.** Seen only at the head of Dry Creek in a snowbank area adjacent to a fir community. June-July. 17237.

***Arnica cordifolia* Hook.** Occasional in white fir and Douglas-fir communities. June. 15612, 15617.

***Artemisia arbuscula* Nutt.** Abundant to dominant on exposed slopes and ridges at the upper edge of and above the pinyon-juniper zone. August-September. 15130, 15254, 16457, 16466.

***Artemisia dracunculus* L.** Collected at the mouth of Lyman Canyon in Oak Creek. Sagebrush community. August-October. 17961.

Artemisia ludoviciana **Nutt. var.** ***incompta*** **(Nutt.) Cronq.** Occasional at the upper edge and above the pinyon-juniper zone, usually in rocky places. August–October. 15136, 15137, 16461.

Artemisia ludoviciana **Nutt. var.** ***ludoviciana.*** Occasional along drainages and in rocky places mostly in the pinyon-juniper zone. August–October. 1490, 15245.

Artemisia nova **A. Nels.** Abundant to dominant on shallow rocky soils on slopes and ridges in and below the pinyon-juniper zone, and occasionally extending to the upper edge and perhaps above this zone, especially on limestone. September–October. 15148, 15233, 15292, 16467.

Artemisia tridentata **Nutt. ssp.** ***tridentata.*** Abundant to dominant on deep alluvial soils of drainage ways in and below the pinyon-juniper zone. September–October. 16380.

Artemisia tridentata **Nutt. ssp.** ***vaseyana*** **Beetle.** Common to abundant over much of the area near the lower fringe of the juniper zone, to the crest of canyon range, in many plant communities; most common and sometimes the dominant plant on concave positions of slopes. September–October. 16454, 16455, 16458.

Artemisiac tridentata **Nutt. ssp.** ***wyomingensis*** **Beetle & Young.** Common to dominant on soils with a hardpan of some type from about 30 to 55 cm (12 to 22 inches) below the surface, mostly below the pinyon-juniper zone and most common beyond the boundary of the area, such as in Little Valley. September.

Aster perelegans **Nels. & Macbr.** Occasional to very locally common in mountainbrush communities. July–September. 14924, 17354, 17953, 17957.

Aster wasatchensis **(Jones) Blake.** Seen at only a few stations among rocks near the crest of the range. August–September. 15135.

Balsamorhiza saggittata **(Pursh) Nutt.** Abundant on open slopes, with big sagebrush and Gambel oak, dominant understory plant in curlleaf mountain mahogany communities, and sometimes in other communities in and above the pinyon-juniper zone. Late May–June. 14034, 15381.

Brickellia californica **(T. & G.) Gray.** Seen on slopes above Wide Canyon, southeast exposure of outcrop of Precambrian quartzite, mountain brush community. 16462.

Brickellia grandiflora **(Hook.) Nutt.** Occasional to locally common in rocky places in mountain brush communities. July–September. 14430, 14926.

Brickellia microphylla **(Nutt.) Gray.** Seen only at a single station near the southern limit of the area in cracks of rocks within a black sagebrush–bluebunch wheatgrass community. July–September. 15232.

Chaenactis douglasii **(Hook.) H. & A.** Occasional in many plant communities throughout the area. May–June. 13901, 13916, 13938, 13951, 14084.

Chrysothamnus greenei **(Gray) Greene.** Collected from adjacent to the area in the Clay Springs drainage from aeolian sand. August–September. 15249.

Chrysothamnus nauseosus **(Pallus) Britt. ssp.** ***hololeucus*** **(Gray) H. & C.** Apparently uncommon in mountain brush and Vasey sagebrush communities. 16459, 17960.

Chrysothamnus nauseosus **(Pall.) Britt. ssp.** ***graveolens*** **(Nutt.) Piper.** Common to abundant, especially along drainages in sagebrush and pinyon-juniper communities. August–October. 16381, 16382, 16385.

Chrysothamnus nauseosus **(Pall.) Britt. ssp.** ***turbinatus*** **(Jones) H. & C.** Abundant on aeolian sand in and below the pinyon-juniper zone along the west side of the area, mostly outside the boundary. August–September. 16386, 17963.

Chrysothamnus viscidiflorus **(Hook.) Nutt. ssp.** ***puberulus*** **(D.C. Eaton) H.& C.** Common to abundant in pinyon-juniper and sagebrush communities, mostly on slopes and ridges. July–August. 14306, 14947, 15149, 15234.

Chrysothamnus viscidiflorus **(Hook.) Nutt. ssp.** ***viscidiflorus.*** Occasional at the south end of the area and perhaps elsewhere in juniper and vasey sagebrush communities.

Cirsium neomexicanum **Gray.** Occasional to locally common in sagebrush and juniper communities. June–August. 16876, 17133.

Cirsium vulgare **(Savi) Ten.** Introduced from the Old World, adventive on disturbed ground, many plant communities. June–July. Seen but not collected.

Cirsium wheeleri **(Gray) Petrak.** Occasional in Gambel oak communities. July. 15792, 17311.

Conza canadensis **(L.) Cronq.** Seen at the mouth of Oak Creek Canyon and upper Lyman Canyon in burnedover cottonwood-willow-oak and mountain brush communities. May–September. 17325, 17952.

Crepis acuminata **Nutt.** Occasional in Vasey sagebrush, pinyon-juniper, and mountain brush communities. June. 14036, 14083, 15634.

Crepis modocensislo Greene. Infrequent in mountain brush and low sagebrush communities. June–July. 14011, 14365.

Crepis occidentalis **Nutt.** Occasional in pinyon-juniper and mountain brush communities. June. 13925, 14037, 14132, 14172.

Erigeron aphanactis **(Gray) Greene.** Collected at a single station at the north end of the Canyon Mountains. Common just east of the area. June. 14045.

Erigeron argentatus **Greene.** Seen at the divide between Oak and Little Oak Creeks on rocky ridge with curlleaf mountain mahogany; also seen adjacent to the area on deposits of old Lake Bonneville above the Sevier River in Mills Valley. 14331.

Erigeron divergens **T. &. G.** Occasional in oak and sagebrush communities, often along canyon bottoms, and perhaps adventive on disturbed ground. June–July. 14017, 14432, 15239, 15820, 16874; Foster 6535.

Erigeron eatonii **Gray.** Occasional in various plant communities above the pinyon-juniper zone. 14029, 14356, 15373, 15556, 15608, 17238; Foster 6529.

Erigeron engelmanii **A. Nels.** Occasional in juniper-sagebrush communities. May–June. 13770, 13794, 13818, 13846, 14109, 16824.

Erigeron flagellaris **Gray.** Occasional along canyon bottoms with narrowleaf cottonwood, oak, and maple. June–July. 14291, 14295; Welsh et al. 17439.

Erigeron nauseosus **(Jones) Cronq.** Occasional in rocky places, often on faces of rock outcrops, usually in mountain brush communities. June–August and to October, with sufficient fall moisture. 15242, 15589, 15596, 15626, 15795, 16083, 16465; Foster 6531.

Erigeron speciosus **(Lindl.) DC.** Occasional to locally common in mountain brush and aspen communities. July–August. 14923, 17353, 17955.

Gnaphalium palustre **Nutt.** Seen only at East Fork Eightmile Creek along canyon bottom with oak, narrowleaf cottonwood, and white fir. July. 14448.

Haplopappus acaulis **(Nutt.) Gray.** Occasional to locally common rocky exposed slopes and ridges in pinyon-juniper and mountain brush and low sagebrush communities; perhaps most common in the northern half of the Canyon Mountains. May–June. 15366, 16841.

Haplopappus armerioides **(Nutt.) Gray.** Seen only near or along the divide between Weetches Canyon and Dry Canyon among rocks and ledges in mountain brush and white fir-Douglas-fir communities. June–July. 15796, 15810.

Haplopappus watsonii **Gray.** Widespread and common throughout the Canyon Mountains in cracks of rock outcrops at the upper edge of the pinyon-juniper zone to near the crest of the mountains. August–October. Intergrading into *H. rydbergii* Blake in Tidestr. 14930, 15132, 15140, 15236, 15241, 15244, 15251, 16081, 16460, 16464, 17951.

Helenthella uniflora **(Nutt.) T. & G.** Occasional in mountain brush communities. June–August. 14431.

Helianthus annus **L.** Adventive on disturbed ground usually in and below the pinyon-juniper zone. 15640, 16383.

Heliomeris multiflora **Nutt.** Occasional in rocky places in mountain brush communities. August–September. 14931, 15824.

Hymenopappus filifolius **Hook.** Occasional in pinyon-juniper communities, infrequent in dry mountain brush communities. Late May–June. 13919, 13950, 14098, 14180; Foster 6544; Welsh 17025.

Hymenoxys acaulis **(Pursh) Parker.** Occasional in juniper communities, locally common in low sagebrush communities. May–June. 13947, 15397.

Hymenoxys cooperi **(Gray) Cockerell.** Occasional on old Lake Bonneville deposits of sandy clay above the Sevier River at the extreme northern limit of the area. May–June. 13835.

Iva axillaris **Pursh.** Infrequent in various plant communities, usually in and below the pinyon-juniper zone. June–July. 14088.

Layia glandulosa **(Hook.) H.& A.** Seen only on sandy ground in the Clay Springs Wash in juniper-sagebrush communities. May–June. 14159, 15309, 15566.

Lactuca serriola **L.** Introduced from the Old World, adventive on disturbed ground and locally common on charred ground where piles of pinyon and juniper slash have been burned after chaining. June–July.

Leucelene ericoides **(Torr.) Greene.** Occasional to locally common in sagebrush-juniper communities. June. 14039.

Lygodesmia grandiflora **(Nutt.) T. & G.** Occasional in sagebrush-juniper communities, usually on sandy soil; seen only at the southwest part of the area. May–June. 14127; Foster 6550.

Macheranthera canescens **(Pursh) Gray.** Occasional in many plant communities. August–October. 14938, 15129, 15243, 16389, 17956.

Macheranthera grindelioides **(Nutt.) Shinners.** Seen at the divide between Oak and Little Oak creeks, on rocky ridge with curlleaf mountain mahogany; common adjacent to the area on old river deposits above the Sevier River on hills between Little Valley and Mills Valley. June–July. 14330.

Macheranthera kingii **(D.C. Eaton) Cronq. & Keck var. *barnebyi* Welsh & Goodrich.** Infrequent to locally common in crevices of cliffs and ledges of precambrian quartzite from mountain brush zone to the crest of the Canyon Mountains. August–September. 14929, 14933, 15133, 15134.

Malacothrix torreyi **Gray.** Infrequent in juniper-sagebrush communities. June. 14149.

Microseris nutans **(Geyer) Schultz-Bip.** Occasional to locally common in oak communities. June. 14012.

Perityle stansburyi **(Gray) Macbr.** Seen only near the northern limit of the area on a limestone outcrop with scattered juniper and black sagebrush. June. 15638.

Petradoria pumila **(Nutt.) Greene.** Common to abundant on rocky exposed slopes and ridges in low sagebrush, pinyon-juniper, and mountain brush communities; infrequent in nonrocky areas. June–August. 14100, 14182, 14321, 14324; Welsh et al. 17451.

Senecio douglasii **DC.** A single large plant found along a roadside at the south end of the Canyon Mountains. July–September. 17364.

Senecio integerrimus **Nutt.** Occasional to locally common in Vasey sagebrush and mountain brush communities. May–June. 15384.

Senecio multilobatus **T.& G. ex Gray.** Occasional in many plant communities over a wide elevational range. May–August. 13981, 14116, 15692, 16840.

Senecio streptanthifolius **Greene.** Seen on Blue Mountain and in Hardscrabble Canyon, pinyon-juniper and mountain brush communities. June. 15555, 168408.

Solidago sparsiflora **Gray.** Occasional to locally common on rock outcrops in the mountain brush zone. August–September. 14437, 14925, 14934, 15138, 15237, 16085, 17359, 17950.

Sonchus asper (L.) Hill. Introduced from the Old World, more or less weedy; seen only once at Eightmile Ditch, disturbed ground. June–September. 16875.

Sphaeromeria diversifolia **(D.C. Eaton) Rydb.** Occasional to locally common in crevices of ledges and cliff, usually above the pinyon-juniper zone. July–September. 14322, 14349, 14935, 15139, 16082.

Stephanomeria exigua **Nutt.** Infrequent or locally common on sandy ground (often stabilized dunes) in the pinyon-juniper zone. June. 14223, 14232; Foster 6549.

Taraxacum officinale **Weber in Wiggers.** Introduced from the Old World, adventive on disturbed ground usually in and below the pinyon-juniper zone. May–October. 13905.

Tetradymia canescens **DC.** Occasional in sagebrush, pinyon-juniper, and dry mountain brush communities. June–August. 14948.

Townsendia florifer **(Hook.) Gray.** Seen at two stations in Clay Springs Wash on aeolian sand. May–June. 14151, 14226.

Tragopogon dubius **Scop.** Introduced from the Old World, adventive on disturbed ground and in various indigenous plant communities. June. 13963.

Wyethia amplexicaulis **(Nutt.) Nutt.** Seen only in Fool Creek drainage where locally abundant in sagebrush-mountain brush communities. May–June. 15623.

Xanthocephalum strumarium **L.** Collected along Highway 132 at the north edge of the area. August–September. 17964.

Xanthocephalum petradoria **Welsh & Goodrich.** Locally common on rocky slopes and ridges, mostly in the mountain brush zone. August–October. 14928, 15127, 15131, 15145, 15240, 15256, 15257, 16080.

Xanthocephalum sarothrae (Pursh) Shinners. Common to abundant in pinyon-juniper communities especially on shallow soils; infrequent to occasional in many other plant communities; adventive on disturbed ground. August–October. 14943, 15128.

Berberidaceae

Mahonia repens G. Don. Occasional in mountain brush and aspen communities. April–May. 13725; Welsh 16401.

Boraginaceae

Amsinckia intermedia Fisch. & Mey. Seen only at two stations on aeolian sand along the south and west sides of the Canyon Mountains. May–June. 15310; Welsh 16590.

Cryptantha compacta Higgins. Occasional in rocky places along the crest of the Canyon Mountains. June–July. 14364, 15554, 15607.

Cryptantha circumscissa (H. & A.) Johnst. Infrequent or occasional on aeolian sand; seen only at the south and west edge of the area in and below the pinyon-juniper zone. May–June. 14118, 14152.

Cryptantha confertiflora (Greene) Payson. Seen at only one location at the extreme western limit of the area on aeolian sand, in a juniper community. June. 15314.

Cryptantha flavoculata (A. Nels.) Payson. Occasional to common in upper pinyon-juniper and mountain brush communities, particularly with curlleaf mountain mahogany. May–June. 14166, 15362, 15560.

Cryptantha gracilis Osterh. Occasional to frequent in sagebrush and pinyon-juniper communities. May–June. 13895, 14157, 15689.

Cryptantha humilis (Gray) Payson. Occasional to common in sagebrush and pinyon-juniper communities. May–June. 13767, 13836, 13945, 15347; Welsh 16417.

Cryptantha kelseyana Greene. Occasional to common, sandy ground in the vicinity of Clay Springs Wash. May–June. 14153, 14224.

Cryptantha pterocarya (Torr.) Greene. Occasional to common in sagebrush and pinyon-juniper communities. May–June. 13842, 14119.

Cryptantha watsonii (Gray) Greene. Occasional in pinyon-juniper, mountain brush, and sagebrush communities. May–June. 15833.

Cynoglossum officinale L. Adventive on disturbed ground, in various plant communities. June–July. 14215.

Hackelia patens (Nutt.) Johnst. Seen only at a canyon on south side of Leamington Canyon, pinyon-juniper community. May–June. 15361.

Lappula occidentalis (Wats.) Greene. Occasional in various plant communities. May–June. 14124.

Lithospermum incisum Lehm. Occasional to common in sagebrush and juniper communities, perhaps most common in Church Mountains. May–June. 13766, 13787, 13897. ***Lithospermum ruderale*** Dougl. ex Lehm. Infrequent in various plant communities over a rather wide elevational range. June–July. 15625.

Mertensia oblongifolia (Nutt.) G. Don. Occasional in upper pinyon-juniper and mountain brush communities. May–June. 14170, 15364, 15614.

Brassicaceae

Alyssum alyssioides L. Introduced from Europe, somewhat weedy and perpetuated by disturbance, in and below the pinyon-juniper zone. May–June. 14206.

Alyssum desertorum Stapf. Introduced from the Old World, somewhat weedy and perpetuated by disturbance, mostly in and below the pinyon-juniper zone. May–June. 13911.

Arabis drummondii Gray. Infrequent in various plant communities, mostly in and above the oak zone. May–June. 14362, 15385; Welsh et al. 17041, 17442.

Arabis glabra (L.) Bernh. Collected only from Oak Creek, cottonwood-oak-maple community. May–July. 17363.

Arabis holboellii Hornem. Occasional in various plant communities over a wide elevational range. May–June. 13903, 15365; Welsh 16593; Welsh et al. 17440.

Arabis microphylla Nutt. Seen at a single station, in cracks of rocks in Oak Creek Canyon. May–June. 15319.

Arabis pendulina Greene. Occasional and locally common in cracks of rock outcrops and on windswept ridges in low sagebrush communities, mostly above 2285 m (7500 ft) elevation. May–June. 14363, 15395, 15552, 15591.

Arabis perennans Wats. Occasional in various plant communities, often in rocky places. May–June. 13840, 14019, 15318, 15599; Welsh 16400.

Arabis pulchra Nutt. in T. & G. Infrequent or occasional in sagebrush and pinyon-juniper communities. May–June. Plants of the area are referable to var. *munciensis* Jones. 13789, 13801, 13832.

Camelina microcarpa Andrz. Introduced from the Old World, adventive on disturbed ground, mostly in and below the pinyon-juniper zone. 13913; Welsh 16602.

Caspella bursa-pastoris (L.) Medic. Introduced from the Old World, adventive on disturbed ground, mostly in and below the pinyon-juniper zone. May–June. 14440, 15296; Welsh 16429.

Cardaria draba (L.) Desv. Introduced from the Old World, adventive, seen only at a few locations in the area. June. 15354.

Chorispora tenella (Pallas) DC. Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. May–June. 15297; Welsh 16428.

Descurainia californica (Gray) Schulz. Infrequent in aspen and fir communities. June–August. 17352.

Descurainia pinnata (Walt.) Britt. Adventive on disturbed ground, in various plant communities. 13793, 13827, 13910, 13920; Welsh 16588.

Descurainia sophia (L.) Webb in Engler & Prantl. Introduced from the Old World, adventive on disturbed ground, mostly in and below the pinyon-juniper zone. 13828.

Draba cuneifolia Nutt. ex T. & G. Infrequent to occasional in pinyon-juniper communities. April–June. 13914, 13974, 14131, 15278, 15298, 15678.

Draba nemorosa L. Occasional in various plant communities usually above the pinyon-juniper zone. April–June. 13996, 14110, 15320, 15399; Welsh 16414.

Draba reptans (Lam.) Fern. With the distribution of *D. cuniefolia* and, except that the upper part of stems and the pedicels glabrous, not different from *D. cuneifolia* April–June. 13968A, 14207, 15298.

Erysismum asperum **(Nutt.) DC.** Occasional in many plant communities over a wide elevational range. May–June. 13769, 13791, 13817; Welsh 16421.

Erysismum repandum **L.** Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. 13810, 13829; Welsh 16412.

Lepidium densiflorum **Schrad.** Seen at Eightmile Creek, juniper community, along an ephemeral drainage. May–June. 14138.

Lepidium lasiocarpum **Nutt. in T. & G.** The one specimen seen (Welsh 16596) is from a pinyon-juniper community at Leamington Pass. May–June.

Lepidium montanum **Nutt. var. *heterophyllum*** **(Wats.) C. L. Hitchc.** Seen only at Lyman Canyon, in cracks of rock outcrops, mountain brush community. June–July. 14316.

Lepidium montanum **Nutt. var. *montanum*** Occasional in sagebrush and pinyon-juniper communities. May–June. 13827, 14095.

Lepidium perfoliatum **L.** Introduced from the Old World, adventive, mostly in and below the pinyon-juniper zone. May–June. 13830.

Lesquerella occidentalis **(Wats.) Wats.** Locally common in upper Lyman Canyon on a massive quartzite outcrop. June. 16883, 17949.

Malcolmia africana **(L.) R. Br. in Ait.** Introduced from Africa, adventive on disturbed ground, usually in and below the pinyon-juniper zone. June. 13957A, 14136.

Physaria chambersii **Rollins.** Occasional to common in sagebrush, pinyon-juniper, and dry mountain brush communities, extending to near the crest of the Canyon Mountains on limestone. May–June. 137982, 13819, 13936, 14097, 15396; Foster 6658.

Sisymbrium altissimum **L.** Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. June–July. 14125.

Stanleya pinnata **(Pursh) Britton.** Infrequent on deposits of Lake Bonneville, above the Sevier River at the extreme northern limit of the area, on seleniferous, alkaline, sandy clay soil. May–June. 14046.

Streptanthella longirostris **(Wats.) Rydb.** Occasional on aeolian sand in sagebrush and juniper communities. June. 14229.

Streptanthus cordatus **Nutt. ex T. & G.** Occasional to frequent in sagebrush and pinyon-juniper communities, infrequent in mountain brush communities. May–June. 13788, 13849, 13939, 13984, 15600; Welsh 16603.

Thelypodium sagittatum **(Nutt.) Endl.** Occasional on sandy clay deposits of old Lake Bonneville above the Sevier River at the north limit of the area. May–June. 15353.

Thlaspi arvensis **L.** Introduced from the Old World, adventive on disturbed areas. May–June. 15572.

Cactaceae

Echinocereus triglochidiatus **Engelm.** Occasional in rocky places, usually within the pinyon-juniper zone. May–June. 15363; Foster 6542; Welsh 16600.

Opuntia polyacantha **Haw.** Occasional in various plant communities except mesic mountain brush, aspen, and fir. June 17134; Foster 6572.

Capparidaceae

Cleome serrulata **Pursh.** Collected from along Highway 132 at the north edge of the area. August–September. 17967.

Caprifoliaceae

Sambucus caerulea **Raf.** Infrequent in pinyon-juniper communities. June–July. 14281; Foster 6551.

Symphoricarpos oreophilus **Gray.** Occasional to common in Vasey sagebrush, aspen, and fir communities. June–July. 14200, 15809.

Caryophyllaceae

Arenaria kingii **(Wats.) Jones.** Occasional to frequent in pinyon-juniper, sagebrush, and mountain brush communities. May–June. 13934, 15346.

Arenaria macradenia **Wats.** Locally common to abundant in mountain brush communities, often in rocky places. June–August. 14173, 14320, 15806, 15831; Welsh et al. 17450.

Lychnis drummondii **(Hook.) Wats.** Seen only in a Vasey sagebrush community at the top of the Canyon Mountains. July. 14334.

Silene antirrhina **(L.) Desv.** Seen in a juniper–black sagebrush community among rocks. May–June. 15355; Welsh et al. 17449a.

Silene douglasii **Hook.** Infrequent in rocky places in mountain brush and white-fir communities. Late June–July. 14424, 15794, 17351.

Stellaria jamesiana **Torr.** Occasional to frequent in mountain brush, aspen, and fir communities. May–July. 13985.

Stellaria media **(L.) Cyrill.** Introduced from the Old World, seen only in Lyman Canyon, wet ground along a small stream in fir-snowberry community. May–September. 17942.

Celastraceae

Forsellesia nevadensis **(Gray) Greene.** Infrequent in rocky places in the pinyon-juniper zone. 15359.

Pachystima myrsinites **(Pursh) Raf.** Occasional in mountain brush, aspen, and fir communities. May–June. 13724, 14032, 14169, 16845.

Chenopodiaceae

Atriplex confertifolia **(Torr. & Frem.) Wats.** Occasional on Lake Bonneville deposits above the Sevier River at the north edge of the area. May–June.

Atriplex falcata **(Jones) Standl.** Occasional on Lake Bonneville deposits of sandy clay above the Sevier River at the north limit of the area. June. 14048.

Chenopodium album **L.** Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. July–August.

Chenopodium botrys **L.** Introduced from the Old World, adventive on disturbed ground, seen in the area on a recent rangeland seeding where juniper had been chained. July–August. 14946.

Chenopodium capitatum **(L.) Asch.** Adventive on disturbed ground in various plant communities over a wide elevational range. June–July. 13993, 14347, 15827, 17347.

Grayia spinosa **(Hook.) Moq. in DC.** Seen only at the northern limit of the area on aeolian sand. May–June. 13851.

Halogeton glomeratus **C. A. Meyer in Ledeb.** Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. July–August. 14233.

Kochia americana **S. Wats.** Occasional on Lake Bonneville deposits of sandy clay above the Sevier River at the extreme northern limit of the area. May–June. 13837, 14047, 15639.

Kochia scoparia **(L.) Schrad.** Introduced, weedy, collected from along Highway 132 at the north edge of the area. August–September. 17965.

Monolepis nuttalliana **(Schult.) Greene.** Occasional in many plant communities over a wide elevational range, usually on disturbed soil. June–August. 13988, 14445.

Salsola iberica **Sennen & Pau.** Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. June–July. 14230.

Sarcobatus vermiculatus **(Hook.) Torr.** Occasional on Lake Bonneville deposits above the Sevier River at the north edge of the area. June–July.

Convolvulaceae

Convolvulus arvensis **L.** Introduced from the Old World, adventive especially on disturbed ground, mostly in and below the pinyon-juniper zone. 14214.

Cornaceae

Cornus stolonifera **Michx.** Occasional along drainages with permanent stream flow. June 13987.

Crassulaceae

Sedum debile **Wats.** Occasional on rock outcrops in and above the pinyon-juniper zone. July. 14312, 14346, 15821, 17356; Welsh et al. 17443.

Sedum lanceolatum **Torr.** The one specimen seen (Foster 6532) is from a sagebrush-juniper community in Oak Creek Canyon. June–July.

Cupressaceae

Juniperus osteosperma **(Torr.) Little.** Dominant overstory plant over much of the area around the base of the mountains, growing on every substrate in the area from sand dunes to cracks of rock outcrops.

Juniperus scopulorum **Sarg.** Occasional in mountain brush communities and with scattered fir. 15375, 15812.

Cyperaceae

Carex aurea **Nutt.** Seen only along a mossy springlet at Ledge Spring. June–August. 17231.

Carex deweyana **Schwein. var. *bolanderi* W. Boott in Wats.** Rare, only a few plants seen at the mouth of Davison Canyon and in Dry Canyon, along permanent streamlets. July. 15826, 17317.

Carex douglasii **F. Boott in Hook.** Occasional, mostly along roads in the pinyon-juniper zone. May–June. 13833.

Carex geyeri **F. Boott.** Occasional to dominant understory plant in oak, aspen, and fir communities. May–June. 13723, 14371, 15374, 15616.

Carex hoodii **F. Boott in Hook.** Rare, moist places, mountain brush communities. 17232, 17358.

Carex microptera **Mack.** Occasional to common along drainages of permanent or near permanent stream flow. June–July. 14194, 14289.

Carex nebrascensis **Dewey.** Very locally common to abundant in wet places. June–July. 14000.

Carex petasata **Dewey.** Infrequent in Vasey sagebrush communities. June–July. 14337.

Carex rossii **F. Boott in Hook.** Occasional to common in many plant communities in and above the pinyon-juniper zone. June. 14016.

Carex vallicola **Dewey.** Occasional in Vasey sagebrush and mountain brush communities. June–July. 14197, 14325, 14434, 15624.

Eleocharis palustris **(L.) R. & S.** Infrequent or very locally common in wet places. June. 14001, 14191.

Elaeagnaceae

Shepherdia argentea **(Pursh) Nutt.** In aeolian sand at the north edge of the area; more common adjacent to the area along the flood plain of the Sevier River. June. 18047.

Ephedraceae

Ephedra nevadensis **Wats.** Occasional in rocky places in the pinyon-juniper zone.

Equisetaceae

Equisetum laevigatum **A. Br.** Infrequent in moist places along drainages. 14195.

Ericaceae

Arctostaphylos patala **Greene.** Locally abundant and sometimes dominant on slopes at the upper edge of the pinyon-juniper zone, up through the mountain brush zone. April–June. 14015, 14939, 15291, 16847.

Euphorbiaceae

Euphorbia glyptosperma **Engelm.** Infrequent or occasional in sagebrush-juniper communities, perhaps most common on sandy soil. June. 14141, 14155.

Euphorbia ocellata **Dur. & Hilg.** Rare on aeolian sand at the southwest part of the area. August–September. 15250.

Fabaceae

Astragalus argophyllus **Nutt. var. *martinii* Jones** Occasional in sagebrush, pinyon-juniper, and oak-maple communities. May–June. 14201, 14332, 15326, 15601; Foster 6518, 6530, 6558.

Astragalus bisulcatus **(Hook.) Gray.** Locally common to abundant on old Lake Bonneville deposits of seleniferous sandy clay or clay ground above the Sevier River at the extreme north limit of the area. June. 14044.

Astragalus calycosus **Torr.** Locally common on old Lake Bonneville deposits of sandy clay above the Sevier River at the extreme north limit of the area; common just to the east of the area. May–June. 13833.

Astragalus ceramicus **Sheld.** Occasional, restricted to aeolian sand in and below the pinyon-juniper zone. June. 14123.

Astragalus cibarius **Sheld.** Occasional to common in sagebrush, pinyon-juniper, and mountain brush communities; one of the most widespread and common loco weeds of the area. May–June. 13785, 13881, 13884, 13940, 15293, 16882; Foster 6528; Welsh 16409.

Astragalus convallarius **Greene.** Occasional in sagebrush, pinyon-juniper, and mountain brush communities. June. 13944, 13962.

Astragalus eurekensis **Jones.** Occasional to common in sagebrush and pinyon-juniper communities, occasional in mountain brush communities. May–June. 13764, 13774, 13784, 13815, 13834, 13952, 15294; Welsh 16419, 16589, 16604.

Astragalus geyeri **Gray.** Rare or infrequent on sandy soils in and below the pinyon-juniper zone. June. 14227.

Astragalus marianus **(Rydb.) Barneby.** Infrequent in various plant communities, at the upper edge and above the pinyon-juniper zone. June–July. 16886; Welsh 16433.

Astragalus oophorus **Wats.** Occasional to common in sagebrush and pinyon-juniper communities. May–June. 13816, 13887, 15352; Welsh 16444, 16587.

Astragalus scopulorum **T. C. Porter.** Infrequent in mountain brush, aspen, and fir communities. June–July. 14436. 15551.

Astragalus utahensis **(Torr.) T. & G.** Occasional to locally abundant in sagebrush and pinyon-juniper communities. May–June. 13765, 13806, 13953, 15351, 15397; Welsh 16403.

Hedysarum boreale **Nutt.** Seen only at the north limit of the area on old Lake Bonneville deposits of sandy clay above the Sevier River, juniper community. May–June. 15349.

Lathyrus brachycalyx **Rydb.** Occasional to common in sagebrush, pinyon-juniper, and mountain brush communities. May–June. 13808, 13949, 14025, 15333, 15360; Welsh 16402, 16407, 16408.

Lathyrus lanzwertii **Kellogg.** Occasional in mountain brush and aspen communities. June–July. 14024, 14031.

Lathyrus pauciflorus **Fern.** Infrequent in mountain brush and fir-snowberry communities. June–July. 15618, 15799.

Lotus utahensis **Otley.** Occasional in sagebrush and sagebrush-juniper communities, seen only in Church Mountains and south end of Canyon Mountains. June–July. 14085, 14278, 14444.

Lupinus brevicaulis **Wats.** Seen only on aeolian sand at Clay Springs Wash in the pinyon-juniper zone. June–July. 14150, 14225, 14228.

Lupinus prunophilus **Jones.** Occasional in pinyon-juniper communities, seen only on south end of Canyon Mountains. May–June. 14165, 15332.

Lupinus sericeus **Pursh.** Seen only in Oak Creek drainage, sagebrush-oak-white fir community. June–July. Foster 6536; Welsh et al. 17452.

Medicago sativa **L.** Introduced from the Old World, used extensively in rangeland seedings. June–July. 14280.

Psoralea lanceolata **Pursh.** Common to abundant and sometimes dominant on sand dunes in and below the pinyon-juniper zone. June–July. 14144; Foster 6546.

Trifolium andinum **Nutt. in T. & G.** Locally common to abundant on faces of rocks and rock crevices in the mountain brush zone and upward to the highest elevations on the Canyon Mountains, mostly north of Oak Creek. May–June. 14342, 14357, 14932, 15377, 15592, 15606, 15829.

Trifolium gymnocarpon **Nutt. in T. & G.** Seen once along a trail to Lyman Canyon, Vasey sagebrush-white fir community. June. 16881.

Trifolium pratense **L.** Introduced from the Old World, seen around a spring in Eight Mile Canyon. July. 17240.

Trifolium repens **L.** Occasional in moist soil along drainages. May–July. 14188.

Vicia americana **Muhl. ex Willd.** Occasional to frequent in Vasey sagebrush-juniper, mesic mountain brush, and aspen communities. May–June. 13790, 13848, 13880, 14092; Welsh 16539a.

Fagaceae

Quercus gambelii **Nutt.** Common to dominant over much of the mountain brush zone, occasional well down into the pinyon-juniper zone. May–June. 13812, 14942.

Fumariaceae

Corydalis aurea **Willd.** Infrequent in various plant communities, usually above the pinyon-juniper zone, rather adventive on disturbed ground. June. 13986.

Geraniaceae

Erodium cicutarium **(L.) L'Her in Ait.** Introduced from the Old World, adventive with disturbance, occasional in sagebrush and pinyon-juniper communities. May–July. 13798, 13807.

Geranium parryi **(Engelm.) Heller.** Rare, seen only at two locations in cracks of massive quartzite outcrops in East Eightmile Creek. July–August. Plants vary from typical *G. parryi* in having whitish rather than purple petals, and they average somewhat smaller. Similar plants have been found in the Stansbury Mountains farther to the north in Utah (A. Taye & B. Wall 1213 and A. Taye & J. Herrick 1431). These plants may be worthy of varital status. 14423, 14916.

Hydrophyllaceae

Hydrophyllum occidentale **(Wats.) Gray.** Common to dominant understory plant in oak and aspen communities, occasional in other communities above the pinyon-juniper zone. May–June. 13999, 15372.

Phacelia ivesiana **Torr.** Infrequent in juniper-sagebrush communities. May–June. 15564, 15677.

Phacelia linearis **(Pursh) Holz.** Infrequent in pinyon-juniper and mountain brush communities, very locally common on aeolian sand in a pinyon-juniper stand in Whiskey Creek drainage. May–June. 15558, 15565, 16838.

Juncaceae

Juncus articus **Willd.** Occasional to locally common in wet places. June–July. 14002.

Juncus bufonius **L.** Infrequent along ephemeral drainages in pinyon-juniper communities. June. 14086, 14140, 17326.

Juncus ensifolius **Wikstr.** Occasional along permanent streams, around seeps and springs, over a wide elevational range. June–July. 14193, 14284.

Juncus tenuis **Willd.** Infrequent in moist and wet places. June–July. 14288.

Lamiaceae

Agastache urticifolia **(Benth.) Kuntze.** Occasional in mountain brush and aspen communities, locally abundant in snow accumulation areas. June–July. 14361.

Dracocephalum parviflorum **Nutt.** Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. June. 14216, 17321.

Leonarus cardiaca **L.** Introduced from the Old World, adventive; seen only at Oak Creek, on canyon bottom with oak; most abundant where cattle have made beds under oak. June–July. 14313, 17959.

Marrubium vulgare **L.** Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone. June–July. 14164.

Monardella odoratissima **Benth.** Occasional to locally common in rocky places usually in the mountain brush zone. July–September. 14319, 15143, 17357.

Liliaceae

Allium acuminatum **Hook.** Occasional to common in various plant communities over a wide elevational range. May–June. 13961, 14014, 14081.

Allium brandegei **Wats.** Infrequent or occasional in various plant communities, mostly above the pinyon-juniper zone. June–July. 14353, 13989 15069.

Calochortus nuttallii **T. & G.** Occasional to common in sagebrush and pinyon-juniper communities. June. 13968, 13978, 14091, 14105, 14171, 14333, 15690.

Erythronium grandiflorum **Pursh.** Occasional to locally common in various plant communities, usually above the pinyon-juniper zone. April–May. 13991, 15316, 15386; Welsh 16422.

Fritillaria atropurpurea **Nutt.** Infrequent or rare in Vasey sagebrush and mountain brush communities. June–July. 13998, 14338.

Veratrum californicum **Durand.** Very locally common in wet places in Dry Canyon and Bowens Canyon. July–August. 17315.

Zigadenus paniculatus **(Nutt.) Wats.** Occasional to rather common in Vasey sagebrush-juniper, pinyon-juniper, and mountain brush communities. May–June. 13805, 13923, 14120, 14145.

Zigadenus venenosus **Wats.** Seen only at Ledge Spring along a springlet. July. 17226.

Linaceae

Linum perenne **L. var. *lewisii*** **Hulten.** Occasional to common in sagebrush, pinyon-juniper, and mountain brush communities.

Loasaceae

Mentzelia laevicaulis **(Dougl.) T. & G.** Seen only at one location between the Canyon and Church mountains in a juniper-sagebrush community. July–August. 14311.

Mentzelia montana **(A. Davids.) A. Davids.** Occasional in juniper and juniper-sagebrush communities. June–July. 14221, 14112. Much like *M. albicaulis* Dougl., which might also be in the area.

Malvaceae

Iliamna rivularis **(Nutt.) Rydb.** Seen at two stations: Buck Hollow north exposure, white fir-oak-maple community, and mouth of Oak Creek, burned over sagebrush–mountain brush community. June–July. 15602, 17318.

Sphaeralcea coccinea **(Nutt.) Rydb.** Occasional in sagebrush and juniper communities in and below the pinyon-juniper zone. May–June. 13930, 14101.

Sphaeralcea grossulariifolia **(H. & A.) Rydb.** Occasional in sagebrush and juniper communities in and below the pinyon-juniper zone. May–June. 13930, 14101; Welsh 16595.

Oxybaphus linearis **(Pursh) Robins.** A single specimen collected from mouth of Oak Creek-Dry Creek, burned over juniper community. July–September. 17331.

Tripterocalyx micranthus **(Torr.) Hook.** Occasional in sand dunes at the southwest edge of the area. June. 14146.

Onagraceae

Camissonia boothii **(Dougl.) Raven ssp. *alyssoides*** **(H. & A.) Raven.** Rare, seen only at one station at the south end of Canyon Mountains in the pinyon-juniper zone. May–June. 14128.

Epilobium angustifolium **L.** Seen at two locations where very locally common, along streamlets in mountain brush and fir communities. July–August. 17943.

Epilobium brachycarpum **Presl.** Occasional in sagebrush, pinyon-juniper, and mountain brush communities. June, July. 14090, 14142, 14298, 15802.

Epilobium canum **(Greene) Raven ssp. *garrettii*** **(A. Nels.) Raven.** Occasional to common in rocky places, often on rock outcrops in mountain brush communities. July–September. 14315, 14457, 14917; Welsh et al. 17449.

Epilobium ciliatum **Raf.** Occasional in moist places along drainages. June–July. 14190, 15835; Welsh et al. 17446.

Epilobium nevadense **Munz.** Rare in rocky places in mountain brush communities. August–September. 14918, 15144.

Epilobium saximontanum **Hausskn.** Occasional in moist places along drainages. June–July. 15822.

Gayophytum racemosum **T. & G.** Occasional, somewhat adventive on disturbed ground, various plant communities, often on moist soil. June–July. 14303, 14358.

Gayophytum ramosissimum **Nutt.** Occasional, somewhat adventive on disturbed ground, various plant communities, usually on dry soil. June–July. 13964, 14121.

Oenothera caespitosa **Nutt.** Occasional in sagebrush and pinyon-juniper communities. May–June 13954, 14209.

Oenothera pallida **Lindl.** Common to abundant on aeiolian sand and locally dominant on active sand dunes. In and below the pinyon-juniper zone. June–September. 14148, 16388.

Orchidaceae

Habenaria sparsiflora **Wats.** Rather rare in white fir communities. July. 14339, 14344.

Habenaria unalascensis **(Sprengel) Wats.** Seen only at the following location: mouth of Davison Creek in shade of white fir. July. 15828.

Orobanchaceae

Orobanche corymbosa **(Rydb.) Ferris.** Seen only along a trail in a mountain brush community in Lyman Canyon. June–September. 17941.

Orobanche fasciculata **Nutt.** Infrequent in sagebrush and pinyon-juniper communities. June–July. 15568; Foster 6547.

Papaveraceae

Argemone munita **Dur. & Hilg.** Occasional to locally common, in sagebrush and pinyon-juniper communities, mostly along roadsides, in burn areas and other places that have been disturbed. June. 13972, 14038, 14181, 14204.

Pinaceae

Abies concolor **(Gord. & Glend.) Lindl.** Common to dominant at upper elevations mostly on cool exposures.

Pinus edulis **Genelm. in Wisliz.** Dominant overstory plant in the middle and at the upper edge of the pinyon-juniper zone, growing on most, if not all, substrates in the area. May–June.

Pinus monophylla **Torr. & Frem. in Frem.** Locally common in the central canyons of the west side of the Canyon Mountains and occasional on the east side of these mountains, apparently crossing some with *P. edulis* as some trees show single- and two-needle bundles on some twigs. May–June. 15637, 16456.

Pinus ponderosa **Laws.** Planted at Plantation Flat in Oak Creek Canyon, where the trees have done very well. Also seen in Fool Creek. May–June.

Pseudotsuga menziesii **(Mirb.) Franco.** Occasional to co-dominant with white fir at upper elevations, usually on cool exposures. May–June. 15562.

Plantaginaceae

Plantago lanceolata **L.** Introduced from the Old World, seen at the mouth of Oak Creek Canyon, burned over cottonwood-willow-oak community. July. 17319.

Poaceae

Aegilops cylindrica **Host.** Introduced from the Old World, seen along a roadside at the mouth of Oak Creek. June. 18733.

Agropyron cristatum **(L.) Gaertn.** Introduced from the Old World, used extensively in rangeland seedings in pinyon-juniper and sagebrush communities. May–June. 13912.

Agropyron dasystachyum **(Hook.) Scribn.** Infrequent in various plant communities in and above the pinyon-juniper zone. June. 13967.

Agropyron intermedium **(Host) Beauv. var. *intermedium*.** Introduced from the Old World, used extensively in rangeland seedings in pinyon-juniper and sagebrush communities. Late May–July. 14279, 14304.

Agropyron intermedium **(Host) Beauv. var. *trichophorum*** **(Link) Halacsy.** Introduced from the Old World, used extensively in rangeland seedings in pinyon-juniper and sagebrush communities. Late May–July. 14304.

Agropyron smithii **Rydb.** Locally common to abundant along swales with moderately deep and somewhat fine-textured soils in the Church Mountains and south end of Canyon Mountains, pinyon-juniper and sagebrush communities. June–July. 14089, 14279.

Agropyron spicatum **(Pursh) Scribn. & Smith.** Co-dominant with sagebrush and often the dominant understory plant in pinyon-juniper communities, increases rapidly after fire, occurs in awned and awnless forms. May–June. 13844, 13922, 13921.

Agropyron trachycaulum **(Link) Malte.** Locally common in Vasey sagebrush, aspen, and fir communities, locally abundant in areas of snow accumulation. June–August. 14367, 15804.

Alopecurus aequalis **Sobol.** Seen along the stream at the mouth of Oak Creek Canyon. June–August. 17328.

Bouteloua gracilis **(H. B. K.) Lag. ex Steud.** Infrequent to very locally common in rocky places in low sagebrush and mountain brush communities near the crest of the range. August–September. 15146.

Bromus brizaeformis **Fisch. & Mey.** Introduced from Europe, seen only at one station on southwest exposure in a sparsely vegetated mountain brush community. May–June. 15573.

Bromus carinatus **H. & A.** Occasional to locally abundant in Vasey sagebrush, aspen, and mountain brush communities at upper elevations and often in snow accumulation areas. June–July. 14018, 15803.

Bromus diandrus **Roth.** Introduced from the Old World, seen only on disturbed ground around Mud Spring, pinyon-juniper-oak community. May–June. 14210.

Bromus hordeaceus **L.** Introduced from the Old World, adventive on disturbed ground in and below the pinyon-juniper zone, apparently quite limited in the area. May–June. 14211, 14286, 14294.

Bromus inermis **Leyss.** Introduced from the Old World, used in rangeland seedings, best adapted for cooler, more moist environments than pinyon-juniper communities, but occasional seeding in such communities. June–July. 13942.

Bromus rubens **L.** Seen only at two stations where locally common in pinyon-juniper-mountain brush communities, on south and southwest exposures. May–June. 15357, 15574.

Bromus tectorum **L.** Introduced from the Old World, adventive on disturbed ground in many plant communities, but most common in and below the pinyon-juniper zone. May–June. 13795; Welsh 16601.

***Dactylis glomerata* L.** Introduced from the Old World, used in rangeland seedings, best adapted for sites that are more mesic than pinyon-juniper communities, but occasionally seeded in such areas. June 13941.

***Danthonia unispicata* (Thurb.) Munro ex Macoun.** Infrequent in dry rock places in mountain brush communities. July. 14351, 14428.

***Elymus cinereus* Scribn. & Merr.** Apparently rare, seen in Oak Creek Canyon near the mouth of Lyman Canyon, Vasey sagebrush-oak community. June–August.

***Elymus glaucus* Buckl.** Infrequent in shade of aspen and cottonwood, usually along drainages. June–July. 14301, 17327.

***Elymus junceus* Fisch.** Introduced from the Old World, used in rangeland seedings in sagebrush and pinyon-juniper communities. June. 16826.

***Festuca ovina* L.** Infrequent in juniper and perhaps mountain brush communities. May–June. 16828.

***Festuca pratensis* Huds.** Introduced from the Old World, seen around a spring in Eightmile Canyon. June–August. 17241.

***Glyceria striata* (Lam.) A. S. Hitch.** Infrequent along permanent streams in canyons. June–July. 14287.

***Hilaria jamesii* (Torr.) Benth.** Infrequent to occasional in juniper-sagebrush communities, perhaps most common in the Church Mountains and extreme south limit of the Canyon Mountains. June. 13970, 14129.

***Hordeum murinum* Huds.** Introduced from the Old World, seen only at Oak Creek Campground. May–July. 17363.

***Melica bulbosa* Geyer ex Port. & Coult.** Occasional in Vasey sagebrush and mountain brush communities. June–July. 14023.

***Muhlenbergia wrightii* Vasey in Coult.** Rather rare along or near the crest of the Canyon Mountains on rock outcrops. September. 15147, 17948.

***Oryzopsis hymenoides* (R. & S.) Ricker in Piper.** Occasional to common in sagebrush, pinyon-juniper, and mountain brush communities. June–July. 13983.

***Oryzopsis micrantha* (Trin. & Rupr.) Thurb.** Rare in rocky places in mountain brush communities and with scattered fir. July. 14343, 15811.

***Phleum pratense* L.** Introduced from the Old World, used in rangeland seedings, best adapted for areas more mesic than pinyon-juniper communities. June. 14179.

***Poa annua* L.** Introduced from the Old World, adventive on disturbed ground, often along ephemeral and permanent streams, and around springs. June–July. 14004, 14446, 15588.

***Poa bulbosa* L.** Introduced from the Old World, adventive on disturbed ground, mostly in and below the pinyon-juniper zone, used in the past for seeding rangelands. 13780, 13796, 13904, 13907, 13977, 14130.

***Poa fendleriana* (Steud.) Vasey.** Common in pinyon-juniper, Vasey sagebrush, and mountain brush communities. April–June. 13809, 14028, 15327, 15328; Welsh 16398.

***Poa pratensis* L.** Occasional to locally common along drainages.

***Poa secunda* Presl.** Common to abundant in sagebrush and pinyon-juniper communities. April–June. 13773, 13896, 13908, 15801; Welsh 16399, 16586.

Polypogon semiverticillatus (Forsk.) Hylander. Seen only in moist ground around Mud Spring and mouth of Oak Creek Canyon. June–July. 14212, 17329.

***Secale cereale* L.** Introduced from the Old World, adventive on disturbed ground, sometimes cultivated as a cereal crop, used in the past for seeding rangelands in sagebrush and juniper communities. May–June. 13926, 16827.

***Sitanion hystrix* (Nutt.) J. G. Sm.** Occasional to common in many plant communities over a wide elevational range. May–June. 13937.

***Sporobolus cryptandrus* (Torr.) Gray.** Occasional on sandy ground, seen only in Church Mountains and south end of Canyon Mountains in and below the pinyon-juniper zone. July–September. 14126.

***Stipa columbiana* Macoun (*S. nelsoni* Scribn.).** Occasional in Vasey sagebrush and aspen communities, usually above the pinyon-juniper zone. June–July. 14022, 14198, 14335, 15633, 15805.

***Stipa comata* Trin. & Rupr.** Occasional in sagebrush and pinyon-juniper communities, usually on sandy soil. May–June. 13969.

***Stipa lettermanii* Vasey.** Occasional in Vasey sagebrush and mountain brush communities above the pinyon-juniper zone. June–July. 14336.

***Vulpia octoflora* (Walt.) Britt.** Infrequent in sagebrush and pinyon-juniper communities. May–June. 13891, 13971.

Polemoniaceae

***Collomia linearis* Nutt.** Occasional in Vasey sagebrush and mountain brush communities. May–June. 14026.

***Eriastrum diffusum* (Gray) Mason.** Seen only at Clay Springs Wash, chainedover juniper woodland, sandy soil; specimen has anthers (0.4–0.6 mm long) and the habit of *E. diffusum*, but the lobes of the leaves are like those in *E. sparsiflorum* (Eastw.) Mason. May–June. 14154.

***Gilia aggregata* Pursh Spreng.** Occasional to rather common in sagebrush and pinyon-juniper communities. June–September. 13935.

***Gilia inconspicua* (J. E. Sm.) Sweet .** Occasional to rather common in sagebrush and pinyon-juniper communities. May–June. 13892, 13943, 13979, 13982.

***Gilia leptomeria* Gray.** Occasional to rather common in sagebrush and pinyon-juniper communities, apparently increasisng after chaining of juniper stands. May–June. 13939, 13946, 14096, 14162, 15688.

***Gilia polycladon* Torr. in Emory.** Occasional just to the east of the area in Little Valley, and to be expected on the area on sandy soils in sagebrush and pinyon-juniper communities at lower elevations.

***Leptodactylon pungens* (Torr.) Nutt.** Occasional in many plant communities over a rather wide elevational range. May–June. 13915, 14094.

***Microsteris gracilis* (Hook.) Greene.** Occasional to common in juniper and juniper-sagebrush communities, increasing with disturbance and locally abundant on chained areas. May–June. 13776, 13965; Welsh 16413.

***Phlox austromontana* Cov.** Infrequent and local in pinyon juniper-juniper and mountain brush communities, usually in rocky places. April–June. 13843, 15289; Welsh 16418.

***Phlox hoodii* Richards.** Occasional in sagebrush and pinyon-juniper communities. March–May. 13783, 13811.

***Phlox longifolia* Nutt.** Occasional in sagebrush, pinyon-juniper, and mountain brush communities. May–June. 13772, 13797; Foster 6541; Welsh 16406.

Polygonaceae

Eriogonum brevicaule Nutt. In many plant communities in and above the pinyon-juniper zone, abundant in rocky places in mountain brush communities and open windswept ridges and slopes. July–October. 14318, 14345, 14368, 14427, 14921, 14922, 15246, 17349, 17350. Small specimens from Fool Peak approach *E. grayi* Reveal, but these are probably depauperate plants of *E. brevicaule*.

Eriogonum cernuum Nutt. Occasional to abundant in sagebrush and pinyon-juniper communities, adventive and increasing on disturbed ground. June–September. 14122, 14143, 14222, 14949; Foster 6545.

Eriogonum heracleoides Nutt. Seen only at a few locations where locally common on rocky slopes in Vasey sagebrush and mountain brush communities. July. 14323, 14429, 17225; Foster 6533.

Eriogonum hookeri Wats. Seen only at one location, in bare soil where a juniper had been uprooted in a chaining. August. 17725.

Eriogonum kearneyi Tidestr. Locally abundant on active and partly stable sand dunes at the west edge of the area; widespread on dunes to the west of the area. August–October. 16387.

Eriogonum maculatum Heller. Locally common on sandy soil in Clay Springs Wash area, apparently increasing after chaining of pinyon and juniper. June–July. 14156, 14220.

Eriogonum microthecum Nutt. Occasional in low sagebrush and mountain brush communities. August–September.

Eriogonum ovalifolium Nutt. Occasional in sagebrush and pinyon-juniper communities. May–June. 13900, 13918, 14099. The yellow flowered phase (var. *multiscapum* Gand.) is common just east of the area.

Eriogonum palmerianum Reveal in Munz. Occasional in sandy soil, most common in Clay Springs Wash area in places cleared of juniper trees by chaining. June–July. 14161, 14219.

Eriogonum racemosum Nutt. Infrequent but widespread within various plant communities over a rather wide elevational range. August–October. 14919, 15141, 17355.

Eriogonum umbellatum Torr. var. **dichrocephalum** Grand. Collected from Weetches Canyon from rocky ground in a Douglas-fir-white fir community. 15797.

Eriogonum umbellatum Torr. var. **umbellatum**. Occasional in pinyon-juniper-sagebrush and mountain brush communities. August. 14920, 14944, 15832.

Polygonum aviculare L. More or less weedy along roads and other areas of disturbance. July–September. 17310.

Polygonum douglasii Greene. Occasional to common, adventive on disturbed ground in many plant communities. June–August. 14302.

Polygonum sawatchense Small. Occasional to locally common, adventive on disturbed ground in many plant communities. June–August. 14139.

Rumex salicifolius Weinm. Infrequent along drainage bottoms in canyons. 14192.

Polypodiaceae

Cystopterus fragilis (L.) Bernh. in Schrader. Infrequent or occasional in rock outcrops, mostly above the pinyon-juniper zone. 14013, 14421, 15604.

Pellaea breweri D.C. Eaton. Infrequent in crevices of ledges. 15813.

Polystichum scopulinum (D.C. Eaton) Maxon. Seen only at East Fork Eightmile Creek, cracks of massive rock outcrop, in mountain brush zone. 14422.

Portulaceae

Claytonia lanceolata Pursh. Occasional in mountain brush communities, and at the edge of aspen and fir communities. April–May. 15290, 15387; Welsh 16431.

Lewisia rediviva Pursh. Occasional on rocky ridges in the mountain brush zone. June–July. 14369.

Montia perfoliata (Donn) Howell. Locally common to abdunant under juniper trees, especially along drainages; occasional in mountain brush and fir communities. Late April–May. 13777, 14113, 15398, 16844; Welsh 16411.

Pyrolaceae

Chimaphila umbellata (L.) Bart. Seen only in one fir community in Davison Canyon. July. 15610.

Pyrola asarifolia Michx. Seen at a single location in a fir community in Davison Canyon. July. 15611.

Pyrola secunda L. Seen only along the crest of the Canyon Mountains above Lyman Canyon. July–August. 17954.

Ranunculaceae

Aconitum columbianum Nutt. In T. & G. Occasional along drainages and around springs; a fairly good indicator of permanent springs and streams. 14438.

Anemone tuberosa Rydb. Seen only at one station at the north end of Canyon Mountains with sagebrush, scattered cliffrose, and juniper. April–May. 15356.

Aquilegia caerulea James. Seen only in cracks of rocks at Weetches Canyon, and along a springlet at Ledge Spring. June–July. 15807, 17228; Foster 6537.

Aquilegia formosa Fisch. in DC. Locally common along drainages where stream flow is permanent or nearly so. June–August. 14300, 15587, 17229.

Delphinium Gray. Infrequent in various plant communities over a wide elevational range. May–June. 13850, 15402A, 15619; Welsh 16594.

Delphinium nuttallianum Pritz. Occasional in sagebrush, pinyon-juniper, and mountain brush communities. May–June. 15383; Welsh 16591.

Delphinium occidentale Wats. Locally common in mesic Vasey sagebrush, mountain brush, and aspen communities; seen at very few stations in the area. July. 14327, 15798.

Myosurus minimus L. Seen only at East Fork Eightmile Creek, among rocks in oak-sagebrush community. June. 14026A.

Ranunculus cymbalaria Pursh. Infrequent in wet places. May–August. 14187; Foster 6539.

Ranunculus sceleratus L. Occasional in seeps, springs, and along streams, in mud and water. May–June. 14189, 14213, 16879, 17322.

Ranunculus testiculatus Crantz. Introduced from the Old World, adventive on disturbed ground, usually in and below the pinyon-juniper zone, common to abundant under juniper. May–June. 13778, 13889.

Thalictrum fendleri Engelm. in Gray. Occasional in rocky snowbank areas and aspen communities. June–July. 14354, 14360, 15593.

Rhamnaceae

Ceanothus martinii **Jones.** Occasional in mountain brush communities. June–July. 14350, 15636, 15834.

Ceanothus velutinus **Dougl. in Hook.** Collected at Eightmile Creek in a mountain brush community. June. 13995.

Rosaceae

Amelanchier alnifolia **(Nutt.) Nutt.** Occasional in mountain brush communities. May–June. 13994, 16880.

Amelanchier utahensis **Koehn.** Occasional in pinyon-juniper and mountain brush communities, mostly on drier sites than *A. alnufolia*. May–June. 16605; Foster 6613.

Cercocarpus ledifolius **Nutt.** Dominant overstory plant over wide areas above the pinyon-juniper zone, on dryer sites than Gambel oak, aspen, or fir; occasional or common in upper pinyon-juniper and other plant communities. May–June.

Cercocarpus montanus Raf. Locally common to abundant in pinyon-juniper and mountain brush communities; the dominant overstory shrub at a few stations such as in Oak Creek Canyon and near Scipio Pass. May–June. Rarely crosses with *C. ledifolius* An apparent hybrid of such origin was found above Wide Canyon. The plant was treelike and had persistent, thick leaves as in *C. ledifolius* but the leaves had the shape and serrations of *C. montanus*. 13820, 15635 (16463, the apparent hybrid).

Cowania mexicana **D. Don. var. *stansburiana* (Torr.) Jeps.** Common to abundant in pinyon-juniper and mountain brush communities, occasionally dominant on slopes and ridges; often associated with black sagebrush on shallow, rocky soils. Late May–June. 14093, 14108, 14307, 15569; Welsh 16599.

Crategus douglasii **Lindl.** Seen at Oak Creek Campground, cottonwood-oak-maple community. May–June. 17361.

Fragaria vesca **L.** Infrequent in various plant communities, usually above the pinyon-juniper zone. June–July. 14426, 17233.

Geum triflorum **Pursh.** Seen only at an ephemeral meadow of forbs at an ecotone between white fir and low sagebrush communities, above divide between Little Oak and Oak Creeks; very locally common. May–June. 15388.

Holodiscus dumosus **(Nutt.) Heller.** Occasional in rocky places in pinyon-juniper and mountain brush communities. June–July. 14469, 17348.

Ivesia gordonii **(Hook.) T. & G. in Newberry.** Seen only at head of Eightmile Creek, rock outcrops, mountain brush-fir zone. June–July. 14936, 17236.

Petrophytum caespitosum **(Nutt.) Rydb.** Very locally common on faces of rock outcrops, probably most common on limestone. July–August. 15830.

Physocarpus malvaceus **(Greene) Kuntze.** Seen only at Buck Hollow and Lyman Canyon, rocky canyon sides, north exposure, white fir-oak-maple community, locally common at both places. June. 15603, 17947.

Potentilla biennis **Greene.** Infrequent along drainage bottoms in the mountain brush zone. June–August. 14433, 15584.

Potentilla concinna **Richards. var. *bicrenata* (Rydb.) Welsh & Johnston** Seen only at the divide between Lyman Canyon and Dry Creek. June. 16887.

Potentilla glandulosa **Lindl.** Occasional in rocky places in mountain brush zone. June–August. 14003, 15595.

Potentilla gracilis **Dougl.** Seen only at the windswept, gravelly pass between Lyman Canyon and Dry Creek. June. 16885.

Prunus virginiana **L.** Occasional and locally abundant along drainages and on slopes in the moutain brush zone. May–June. 13992.

Purshia tridentata **(Pursh) DC.** Occasional to abundant in Vasey sagebrush-juniper, pinyon-juniper, and mountain brush communities; sometimes common on aeolian sand with juniper. May–June. 13898, 13917, 14106, 14107.

Rosa woodsii **Lindl.** Occasional to locally common along drainages. June–July. 14296, 17946.

Rubus leucodermis **Dougl.** Infrequent along drainages, usually in mountain brush and aspen communities. June–July. 14435.

Sanguisorba minor **Scop.** Introduced from the Old World, used in recent rangeland seedings, particularly in the pinyon-juniper zone. June. 15691, 16823.

Rubiaceae

Galium aparine **L.** Occasional to common in pinyon-juniper, oak, and narrowleaf cottonwood communities, often along ephemeral drainages. May–July. 13802, 14009, 14137, 14196, 14447.

Galium bifolium **Wats.** Seen at only one location on a rock outcrop in a mountain brush community near Pauls Meadow. June–July. 15630.

Salicaceae

Populus angustifolia **James.** Common to dominant tree along some drainages of permanent or nearly permanent waterflow. May–June.

Populus tremuloides **Michx.** Common to dominant tree on mesic slopes and along drainages. April–May.

Salix exigua **Nutt. spp. *melanopsis* (Nutt.) Cronq.** Occasional or locally common along drainages; usually in and below the pinyon-juniper zone. April–May.

Salix lasiandra **Benth.** Rather rare, along streams. May–June. 17313.

Salix lasiolepis **Benth.** Infrequent along drainages within the pinyon-juniper and mountain brush zones. April–May. 13990, 15315, 16391, 16829.

Salix lutea **Nutt.** Seen in Oak Creek Canyon, wet places. May–June. 16878.

Salix scouleriana **Barratt in Hook.** Infrequent along drainages in mountain brush, aspen, and fir communities. April–May. 15252, 15622, 17314, 17944.

Santalaceae

Comandra umbellata **(L.) Nutt.** Occasional in many plant communities. May–July. 13831, 13899, 15814.

Saxifragaceae

Heuchera parvifolia **Nutt.** Occasional in pinyon-juniper and mountain brush communities, usually in rocky places. June–July. 14033, 15594, 15598.

Heuchera rubescens **Torr.** Occasional to common in crevices of ledges and cliffs at the upper edge of the pinyon-juniper zone and upward. June–July. 14168, 15597, 15823.

Lithophragma glabra **Nutt.** Infrequent or occasional in sagebrush, pinyon-juniper, and mountain brush communities. April–May. 14353A, 15295, 15321; Welsh 16592.

Lithophragma parviflora **(Hook.) Nutt.** The two specimens seen are from oak communities in Oak Creek Canyon. April–May. 18734; Cottam & McMillan 9616.

Mitella stauropetela **Piper.** Seen only in Eightmile Creek in a white fir community. June. 14425, 17227.

Ribes aureum **Pursh.** Infrequent to very locally common along drainages. May–June. 17453; Welsh et al. 17453.

Ribes cereum **Dougl.** Collected once from Hardscrabble Canyon from a pinyon-juniper-mahogany community. June. 16842.

Ribes velutinum **Greene.** Infrequent, usually in rocky places in the mountain brush zone. June. 14328, 15323; Welsh 16423.

Ribes wolfii **Rothr.** Infrequent, Douglas-fir-white fir communities, usually in rocky places. July. 14372, 17230, 17945.

Saxifraga rhomboidea **Greene.** Seen in a drying meadow of forbs at an ecotone between a low sagebrush and white fir community at the divide between Oak Creek and Little Oak Creek, and in pockets of soil in a massive quartzite outcrop in upper Lyman Canyon. May. 15389, 16884.

Scrophulariaceae

Castilleja chromosa **A. Nels.** Occasional to common in sagebrush, pinyon-juniper, and mountain brush communities. May–June. 13768, 13814, 14030; Welsh 16416.

Castilleja linariifolia **Benth. in DC.** Occasional in Vasey sagebrush and mountain brush communities. June–July. 15142.

Collinsia parviflora **Dougl. ex Lindl.** Occasional to abundant in many plant communities over a wide elevational range. April–June. 13771; Welsh 16415.

Limnosella aquatica **L.** Seen only at East Fork Eightmile Canyon, wet soil along the stream and around springs. 14186.

Mimetanthe pilosa **(Benth.) Greene.** Seen only at West Fork Eightmile Creek, ephemeral drainage bottom in juniper community. June. 14114.

Mumulus guttatus **Fisch.** Occasional in wet places, usually in and above the pinyon-juniper zone. June–August. 14290, 17233.

Nama densum **Lemmon.** Seen only at single location in Whiskey Creek drainage on aeolian sand in a juniper community. June. 15563.

Penstemon angustifolius **Nutt.** Very locally common on aeolian sand in Clay Springs Wash, sagebrush and juniper communities. May–June. 15402, 15403.

Penstemon confusus **A. Nels.** Seen only on old Lake Bonneville deposits of sandy clay above the Sevier River at the extreme north limit of the area. May. 15360.

Penstemon cyananthus **Hook.** Rare in pinyon-juniper, Vasey sagebrush, and mountain brush communities. June–July. 14352, 17239. Plants of the area might be referable to ssp. *longiflorus* Pennell.

Penstemon eatonii **Gray.** Occasional in pinyon-juniper communities. June. 13948, 15567.

Penstemon humilis **Nutt.** Occasional in pinyon-juniper and mountain brush communities, often in rocky places. May–June. 13882, 13893, 14167, 15631, 16825.

Penstemon leonardii **Rydb.** Very locally common in rocky places near the crest of the Canyon Mountains with mountain brush and scattered fir. July. 14340, 15793.

Verbascum thapsus **L.** Occasional, usually in and below the pinyon-juniper zone, adventive on disturbed ground. June–August. 14283.

Veronica americana **Schwein. in DC.** Infrequent, aquatic or in mud. June–August. 14185, 17323.

Veronica anagallis-aquatica **L.** Infrequent, aquatic or in mud. June–August 14183, 17324; Welsh et al. 17445.

Veronica biloba **L.** Common to abundant in many plant communities, most common along drainages and in canyons, adventive on disturbed ground. May–June. 13775, 13890, 13931, 15400; Welsh 16430.

Veronica peregrina **L.** Infrequent along drainages, usually in mountain brush, aspen, or fir communities. June–July. 14184, 14443.

Selaginellaceae

Selaginella watsonii **Underw.** Occasional in rocky places in and above the pinyon-juniper zone. 14355.

Solanaceae

Nicotiana attenuata **Torr.** Occasional to locally common in juniper-sagebrush communities, adventive on disturbed ground, and locally abundant on charred soil where slash piles from chainings have been burned. June–July. 14202.

Solanum triflorum **Nutt.** Occasional adventive on disturbed ground; the few plants seen were in juniper and sagebrush areas that had been chained. June–September. 14163, 14945, 16384.

Ulmaceae

Celtus reticulata **Torr.** Occasional along intermittent drainages of lower West Eightmile Creek. June. 14102.

Urticaceae

Urtica dioica **L. spp. *gracilis* (Ait.) Seland.** Occasional along drainages. June–July.

Valerianaceae

Plectritis macrosera **T. & G.** Occasional and locally common in pinyon-juniper communities and especially under juniper trees and along drainages. May–June. 13799, 13927, 14115; Welsh 16404.

Verbenaceae

Verbena bracteata **Lag. & Rodr.** Common to abundant usually in and below the pinyon-juniper zone, adventive on disturbed ground, and mostly along roads. June–July. 13973, 14087, 14203.

Violaceae

Viola nephrophylla **Greene.** Infrequent along drainages, usually in the mountain brush zone. May–June. 15376.

Viola nuttallii **Pursh var.** ***major*** **Hook.** Seen at two stations in Davison Canyon-Buck Hollow area of Fool Creek drainage, in white fir-aspen-snowberry and oak-maple communities. June. 15613, 15620; Welsh 16426.

Viola purpurea **Kell.** Infrequent along dry drainage bottoms in sagebrush-juniper communities, occasional in rocky snowbank areas up to the crest of the Canyon Mountains. April–June. 13813, 14352a, 15288.

IN VITRO DIGESTIBILITY OF *KOCHIA PROSTRATA* (L.) SCHRAD.[1]

Bruce L. Welch[2] and James N. Davis[2]

ABSTRACT.— In vitro digestibility was determined for 13 accessions of *Kochia prostrata*. Vegetative samples were collected in February and April. No significant differences in digestibility were detected due to month sampled or among accessions. The mean in vitro digestibility of the 13 accessions was 32.2% of dry matter digested. The accessional range was from 20.2 to 38.0% of dry matter digested.

Kochia prostrata, commonly referred to as prostrate summer cypress, is being tested as a potential forage plant for western United States ranges. It was first introduced from Russia during the early 1960s (Keller and Bleak 1974). Limited nutritive studies have been conducted on accessions of *K. prostrata* (Davis 1979). Winter crude protein varied from 5.4 to 10.9% (Davis 1979, Davis and Welch 1984). Winter carotene content varied from 1.3 to 12.1 mg/100 g of dry matter (Davis 1979). Winter digestibility for *K. prostrata* has not been studied. Therefore, we undertook this study to determine the in vitro digestibility of accessions of *K. prostrata* grown on a uniform garden.

MATERIALS AND METHODS

Thirteen accessions of *K. prostrata* were selected to study in vitro digestibility from a uniform garden located at Ephraim, Utah. The source of the genetic materials for the accessions used in this study is given in Table 1. For each accession five plants were selected at random to furnish a composite vegetative sample needed for the digestion trials. The same plants were used throughout the study. Vegetative samples were collected in February and April 1982. During this part of the year, *K. prostrata* plants consist of two types of vegetative tissues, the "upper" and "lower" parts of the stem. The upper stem is that part of the stem where the seed was developed and has since shattered, leaving a dry, brownish, somewhat erect vegetative shoot. The lower stem is that part of the stem where green leaves begin. Both types of tissue were sampled from the selected plants. Samples were ovendried at 100 C for 48 hours. Then they were ground in a Wiley mill, passed through a 1-mm screen, and stored in airtight containers.

We used the in vitro digestibility procedure as outlined by Pearson (1970). Data were expressed as a percent of dry matter digested. A paired t-test was used to detect differences between upper and lower stem samples.

TABLE 1. Plant introduction numbers, U-numbers of the Utah Division of Wildlife Resources W-82-R, soil types, and location for *Kochia prostrata* accessions used in this study.

PI no.	U no.	Soil type	Location
330708	U-1	°	Tehran, Iran
314929	U-2	°	Stavropol, Russia
°	U-3	°	Yun Dudar, Russia
356824	U-5	Salty	Actobinsk, Russia
356823	U-6	Sandy	Actobinsk, Russia
356822	U-7	Clay	Ural Mountains, Russia
356821	U-8	Salty	Actobinsk, Aral Sea, Russia
356825	U-9	Clay	Actobinsk, Russia
356826	U-10	Salty	Actobinsk, Ural Mountains, Russia
356819	U-11	Salty	Actobinsk, Aral Sea, Russia
356820	U-12	Sandy	Actobinsk, Aral Sea, Russia
356818	U-13	Clay	Actobinsk, Aral Sea, Russia
356817	U-14	Salty	Actobinsk, Aral Sea, Russia

°Information not available

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[1] This article was written by a United States government employee and a federal cooperator on official time, and it is therefore in the public domain.

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TABLE 2. In vitro digestibility of the lower vegetative stem samples of *Kochia prostrata* for the months of February and April. Data are pooled for the two months and expressed as a percent of dry matter digested.

Accession no.	% dry matter digested	Accession no.	% dry matter digested
11	28.1	2	32.2
12	28.6	10	33.6
6	28.6	9	33.9
7	29.8	1	36.2
13	30.3	3	36.4
8	31.4	5	38.0

TABLE 3. In vitro digestibility of the upper vegetative stem samples of *Kochia prostrata* for the months of February and April. Data are pooled for the two months and expressed as a percent of dry matter digested.

Accession no.	% dry matter digested	Accession no.	% dry matter digested
11	20.2	12	26.4
6	21.5	8	27.7
7	21.6	1	28.6
9	22.8	2	29.7
10	23.0	5	33.0
13	26.0	3	35.8
14	26.2		

TABLE 4. In vitro digestibility of winter range forages.

Winter forage	Dry matter digestibility (%)	Reference*
Aspen	57.4	1
Big sagebrush	57.3	2,3,4,5,6,7,10
Bud sagebrush	57.0	8
Wood rose	54.5	1
Sand dropseed grass	53.2	8
Black sagebrush	53.1	8
Rose hips	51.1	6,7
Indian rice grass	50.0	8,10
Bluestem wheatgrass	49.6	10
Curl-leaf mahogany	49.1	4,6
Galleta	48.2	8
Needle-and-thread	47.0	10
Bluebunch wheatgrass	45.5	10
Common winterfat	44.7	8
Rubber rabbitbrush	44.4	10
Shadscale	43.4	8
Western snowberry	41.0	1
Chokecherry	38.8	1,11
Fourwing saltbush	38.3	9
Cliffrose	37.6	12
Desert bitterbrush	35.8	12
Prostrate summer cypress	32.2	this study
Apache-plume	29.8	12
Gambel oak	28.1	2
Antelope bitterbrush	25.6	4,6,12
True mahogany	24.4	4,6,10

*1. Dietz 1972.
2. Kufeld et al. 1981.
3. Sheehy 1975.
4. Urness et al. 1977.
5. Wallmo et al. 1977
6. Welch and Pederson 1981.
7. Pederson and Welch 1982.
8. Welch et al. 1983a.
9. Welch and Monsen 1984.
10. Ward 1971.
11. Uresk et al. 1975.
12. Welch et al. 1983b.

RESULTS AND DISCUSSION

No significant differences were detected between months (February and April), or among vegetative stem samples for (upper and lower) accessions. A t-test did show a significant difference between upper and lower vegetative stem samples. The lower samples' in vitro digestibility on an accessional basis ranged from 28.1 to 38.0% of dry matter, with a mean of 32.2 percent (Table 2). In vitro digestibility on an accessional basis for upper vegetative samples ranged from 20.2 to 35.8%, with a mean of 26.3% of the dry matter (Table 3).

As a winter forage, *Kochia prostrata* is low in digestibility (Table 4). It ranks 24th in the winter forages listed in Table 4. Winter crude protein content has been reported to be 8.5% (Davis 1979). Thus, *Kochia prostrata* could be used to increase winter supplies of crude protein while increasing diversity of forage.

LITERATURE CITED

DAVIS, A. M. 1979. Forage quality of prostrate *Kochia* compared with three browse species. Agron. J. 71:822–824.

DAVIS, J. N., AND B. L. WELCH. In press. Seasonal variation in crude protein among accessions of *Kochia prostrata*. *In* Proceedings of the *Atriplex* symposium. USDA, For. Serv. Gen. Tech. Rep. INT-_____. Intermtn. For. and Range Exp. Sta., Ogden, Utah.

DIETZ, D. R. 1972. Nutritive value of shrubs. Pages 289–302 *in* Wildland shrubs—their biology and utilization: a symposium. USDA, For. Serv. Gen. Tech. Rep. INT-1. Intermtn. For. and Range Exp. Sta., Ogden, Utah. 494 pp.

KELLER, W., AND A. T. BLEAK. 1974. *Kochia prostrata*: a shrub for western ranges? Utah Sci. 34:24–25.

KUFELD, R. C., M. STEVENS, AND D. C. BOWDEN. 1981. Winter variation in nutrient and fiber content and in vitro digestibility of gambel oak [*Quercus gambelli*] and big sagebrush [*Artemisia tridentata*] from diversified sites in Colorado. J. Range Manage. 34:149–151.

PEARSON, H. A. 1970. Digestibility trials: in vitro techniques. Pages 85–92 *in* Range and wildlife habitat evaluation—a research symposium. USDA, For. Serv. Misc. Pub. No. 1147. 220 pp.

PEDERSON, J. C., AND B. L. WELCH. 1982. Effects of monoterpenoid exposure on ability of rumen inocula to digest a set of forages. J. Range Manage. 35:500–502.

SHEEHY, D. P. 1975. Relative palatability of seven *Artemisia* taxa tò mule deer and sheep. Unpublished thesis. Oregon State Univ., Corvallis. 147 pp.

URESK, D. W., D. R. DIETZ, AND H. E. MESSNER. 1975. Constituents of in vitro solution contribute differently to dry matter digestibility of deer food species. J. Range Manage. 28:419–421.

URNESS, P. J., A. D. SMITH, AND R. K. WATKINS. 1977. Comparison of in vivo and in vitro dry matter digestibility of mule deer forages. J. Range Manage. 30:119–121.

WALLMO, O. C., L. H. CARPENTER, W. L. REGELIN, R. B. GILL, AND D. L. BAKER. 1977. Evaluation of deer habitat on a nutritional basis. J. Range Manage. 30:122–127.

WARD, L. A. 1971. In vitro digestibility of elk winter forage in southern Wyoming. J. Wildl. Manage. 35:681–688.

WELCH, B. L., AND J. C. PEDERSON. 1981. In vitro digestibility among accessions of big sagebrush by wild mule deer and its relationship to monoterpenoid content. J. Range Manage. 34:497–500.

WELCH, B. L., J. C. PEDERSON, AND W. P. CLARY. 1983a. Ability of different rumen inoculum to digest range forages. J. Wildl. Manage. 47:873–877.

WELCH, B. L., S. B. MONSEN, AND N. L. SHAW. 1983b. Nutritive value of antelope and desert bitterbrush, stansbury cliffrose, and apache-plume. Pages 173–185 *in* Proceedings of the Bitterbrush and Cliffrose Symposium. USDA, For. Serv. Gen. Tech. Rep. INT-152. Intermtn. For. and Range Exp. Sta., Ogden, Utah.

WELCH, B. L., AND S. B. MONSEN. In press. Nutritive value of 43 accessions of fourwing saltbush (*Atriplex canescens*) grown on a uniform garden. *In* Proceedings of the *Atriplex* Symposium. USDA, For. Serv. Gen. Tech. Rep. INT-____. Intermtn. For. and Range Exp. Sta., Ogden, Utah.

HABITAT RELATIONSHIPS OF *GLAUX MARITIMA* IN CENTRAL UTAH

Jack D. Brotherson[1] and Sarah J. Barnes[1]

ABSTRACT.— Thirty-five study sites were established in the meadow communities surrounding Utah Lake in central Utah. The study sites ranged across several community types. *Glaux maritima* was found in all sites but varied as to its ecological importance in these communities. Sixteen soil factors were measured relative to the stands studied. Cover of *Glaux maritima* correlated with parts per million sodium and total soluble salts in the soil. No other factors correlated significantly with the cover of Glaux maritima. *Glaux maritima* occupied only those sites with high levels of moisture throughout the growing season. The high moisture levels came from springs, seeps, elevated water tables, and early seasonal inundation. High levels of Glaux maritima cover corresponded to low numbers of species in the habitat.

Glaux maritima (Sea milkwort) is known in the geological record from organic deposits of Devensian (last glacial) age from England and Europe (Adam 1977). It is a succulent, halophytic forb whose optimal growth occurs in habitats with moderately to highly saline soils. In the northern hemisphere, it is restricted to coastal tidal and inland alkaline marshes and meadowland areas (Hitchcock and Cronquist 1973).

Most of the research on *Glaux maritima* has been done in Europe and has emphasized its physiological and histological characteristics. Rozema and Riphagen (1977) found that the more saline the soil, the more salt was secreted by its salt glands. The structure and function of the salt gland itself was studied in depth by Rozema et al. (1977). Rozema (1975) stated that there was no conclusive evidence to prove that salinity has a stimulating influence on the growth of this species. Carbohydrate concentrations in the hibernacle roots of *G. maritima* were studied by Grandin (1973). Other research on its biology includes salt secretion (Rozema et al. 1981), nitrogen metabolism (Stewart et al. 1973), the effects of sodium chloride and soil water saturation on the development and carbohydrate and mineral content of the plant (Grandin 1981), geographic distribution patterns (Dapper 1969, Rozema 1975, and Toman 1976), population dynamics (Rozema et al. 1978), and soil relationships (Konovov 1978). Little if any has been written on the habitat and community relationships of *Glaux maritima* in North America.

The purpose of this paper is to discuss the habitat and community relationships of *Glaux maritima* in central Utah. An understanding of these factors should be of value to the management of wetland habitats involving this species.

STUDY AREA

The study sites (35) were established in meadows surrounding Utah Lake in Utah County, Utah (Lat. 40°10'N, Long. 11°50'W), where the mean elevation above sea level was 1377 m. Weather information characteristic of the study site is best represented from data taken at the Provo City airport, which lies within the community boundaries being studied. Average temperatures range from 33 C in July, the hottest month, to 3 C in January, the coldest. Precipitation is in the form of both snow and rain, averaging 340 mm annually, with 60% falling during the winter and spring months. The annual precipitation of adjacent mountain ranges averages from 760 to 1270 mm (Morden 1980).

MATERIALS AND METHODS

Thirty-five study sites were randomly selected from saline meadow communities in the Utah Lake area (Fig. 1). A 10 x 10 m

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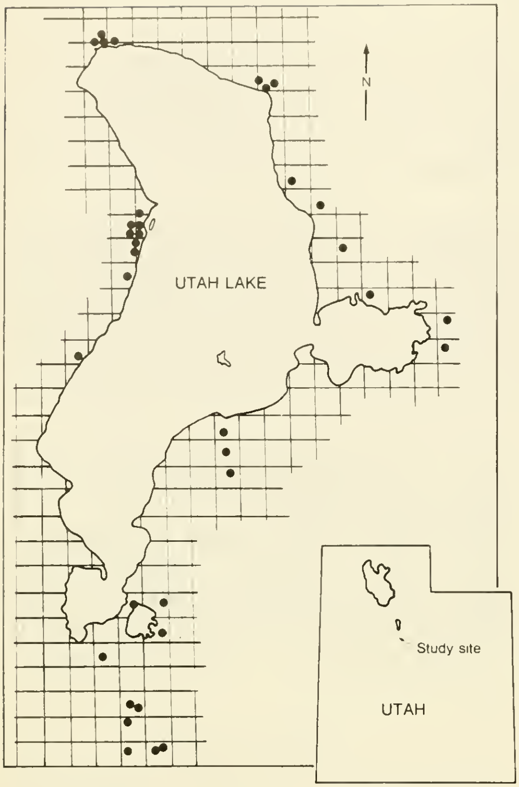

Fig. 1. Map showing the locations of 35 study sites near Utah Lake in central Utah.

study plot (0.01 ha) was established at each site. Study plots were delineated by a cord 40 m long with loops every 10 m for corners. The corners were secured by steel stakes. Each plot was subsampled with twenty 0.25 m^2 quadrats distributed across the surface of the plot in a grid of five evenly spaced transects of four quadrats each. This placement kept the quadrats equal distances from each other and spread them uniformly across the plot.

Total living plant cover, plant cover by life form (i.e., trees, shrubs, subshrubs, perennial forbs, perennial grasses, sedges, rushes, annual grasses, annual forbs, cryptogams), litter, exposed rock, bare soil were ocularly estimated from each quadrat following a procedure suggested by Ostler (1980). Cover for all plant species encountered was also estimated using the cover class categories suggested by Daubenmire (1959). In addition, all species occurring within the study plot but not encountered in the quadrat subsamples were listed and given a percent cover value of 0.01 so they could be included in the overall data analyses.

Three soil samples were taken in each plot (from opposite corners and the center) from the top 20 cm of soil and later combined for laboratory analysis. This depth was considered adequate because Ludwig (1969) in a study of different foothill communities in Utah showed that the surface decimeter of soil when sampled with reference to mineral concentrations yields 80% of the information useful in correlations with plant data. Holmgren and Brewster (1972) also showed in a study of desert shrub communities in western Utah that greater than 50% of the fine roots (those most likely to absorb soil minerals) were found concentrated in the upper 15 cm of the soil profile. With respect to grasslands, Christie (1979) found that the top layer of soil is the region of most active mineral uptake.

The following characteristics were recorded for each plot: elevation (taken from published U.S. Department of Interior Geological Survey 7.5 minute series topographic maps); percent slope; slope position (1 = ridgetop, 2 = midslope, 3 = drainage accumulation area); moisture (1 = dry, 2 = moist, 3 = wet, 4 = seasonally inundated, 5 = submerged); grazing impact (0 = none, 1 = light, 2 = moderate, 3 = heavy).

Soil samples were analyzed for texture (Bouyoucos 1951), pH, soluble salts, mineral composition, and organic matter. Soil reaction was taken with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A 1:1 soil-water paste (Russel 1948) was used to determine pH and total soluble salts. Soils were extracted with 1.0 neutral normal ammonium acetate for the analysis of calcium, magnesium, potassium, and sodium (Jackson 1958, Hesse 1971, Jones 1973). Zinc, manganese, iron, and copper were extracted from the soils by use of DTPA (diethylenetriamine-penta-aceticacid) extracting agent (Lindsay and Norvell 1969). Individual ion concentrations were determined using a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). Soil phosphorus was extracted by sodium bicarbonate (Olsen et al. 1954). Total nitrogen analysis was made using macro-Kjeldahl procedures (Jackson 1958). Organic matter was determined by total carbon measurement via burning 10 grams of soil sample at 950 C in a LECO medium temperature resistance furnace following methods described by Allison (1965).

Plant nomenclature follows Welsh and Moore (1973) for the dicotyledons and Cronquist et al. (1977) for the monocotyledons. Prevalent species (those most frequently encountered during sampling) of the various plant communities are reported as equal to the average number of species per 0.01 ha sampling area examined (Warner and Harper 1972).

Cluster analysis techniques (Sneath and Sokal 1973) were applied to similarity index values (in percent) computed via the formula: $SI = \Sigma \min (XiYi)/\Sigma \max (XiYi)$ where SI is the similarity index between two study sites: the min (XiYi) represents the sum of the minimum values from the paired relative abundance figures across all species found in stands (XY), and the max (XiYi) represents a similar figure for the maximum values of the same two stands (Ruzicka 1958). Clustering the above indices employed unweighted pair group clustering procedures (Sneath and Sokal 1973). This method computes the average similarity of each unit to the cluster, using arithmetic averages. It is widely used and has been found to introduce less distortion than other methods (Kaesler and Cairns 1972). Using this technique we expected to cluster those stands which were most alike together and thus aid in uncovering relationships existent between them.

Data analysis consisted of computing means, standard deviations, and coefficients of variation for all measured biotic and abiotic variables (Ott 1977). Linear regression analysis (Cochran and Snedecar 1976) was applied to the cover values of *Glaux maritima* in relationship to the associated biotic and abiotic factors in the study sites to determine the degree to which they were associated.

Results and Discussion

A total of 110 species were encountered in 35 stands. Of these 110 species, 14 were considered prevalent species and are shown in Table 1. The majority of these species grow on sites of elevated moisture levels in the soil and are to some degree tolerant of salinity and alkalinity.

To assess the relationships of *Glaux maritima* to the communities in which it occurred, a cluster analysis was performed (Fig. 2). The cluster analysis revealed the separation of the stands into six basic groups, with two stands remaining apart from the rest. These two remaining stands were arbitrarily designated as an independent group, because they do not represent any particular community and are not clustered significantly with the other stands.

The Spike Rush Meadow stands (Group 1; Fig. 2) are situated in areas that are often inundated in early seasons of the year and which have a continual water supply (either from springs, seeps, or elevated levels of ground water throughout the growing season). They are dominated primarily by *Eleocharis palustris* and other sedges, with some contribution from perennial grasses and forbs (Table 2).

The Marsh Edge Meadows (Group 5; Fig. 2) constitute a broadly scattered type occurring around the entire perimeter of the Utah Lake marsh as well as being well developed in areas back from the lake where there is constant water accumulation from springs or runoff. The dominant species of this group is *Scirpus pungens*, with *Distichlis spicata*, *Muhlenbergia asperifolia*, and *Trifolium repens* as subdominants (Table 2). Although these meadows are often subjected to in-

Table 1. Prevalent species associated with sites where *Glaux maritima* was found growing.

	Presence (%)	Average Cover (%)	PxC index
Distichlis spicata	77.14	28.12	21.69
Eleocharis palustris	65.71	23.65	15.54
Juncus balticus	74.29	21.70	16.12
Scirpus pungens	45.71	16.03	7.33
Glaux maritima	100.00	14.32	14.32
Carex praegracilis	22.86	6.14	1.40
Elaeagnus angustifolia	25.71	5.76	1.48
Eleocharis rostellata	51.43	4.77	2.45
Crepis runcinata	45.71	4.60	2.10
Hordeum jubatum	68.57	3.97	2.72
Carex aquatilis	14.29	3.81	0.54
Muhlenbergia asperifolia	31.43	3.76	1.18
Agrostis alba	31.43	3.52	1.11
Bromus tectorum	5.71	3.84	0.22

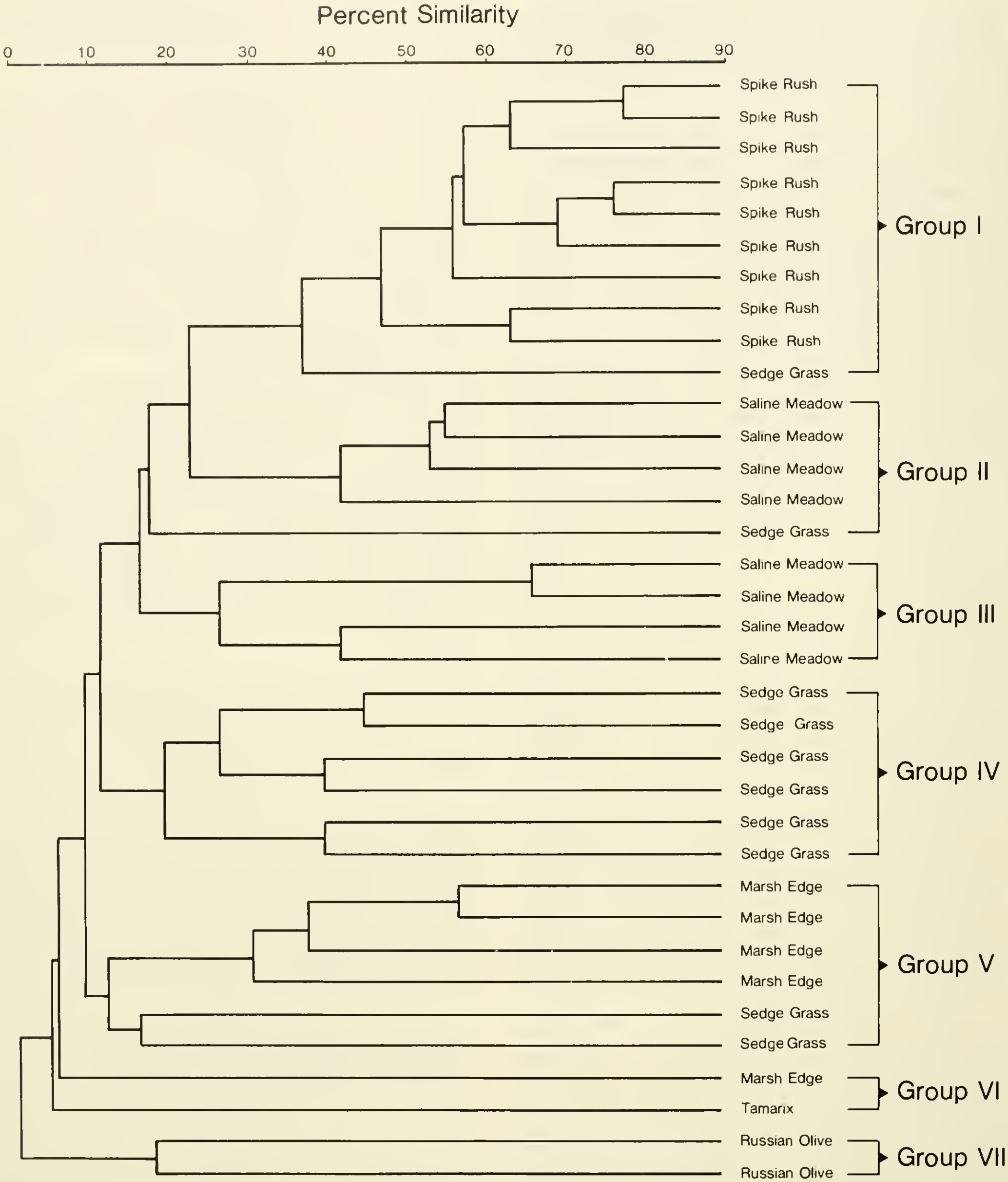
Percent Similarity
0
10
20
30
40
50
60
70
80
90
Spike Rush
Spike Rush
Spike Rush
Spike Rush
Spike Rush
Spike Rush
Spike Rush
Spike Rush
Spike Rush
Sedge Grass
Group I
Saline Meadow
Saline Meadow
Saline Meadow
Saline Meadow
Sedge Grass
Group II
Saline Meadow
Saline Meadow
Saline Meadow
Saline Meadow
Group III
Sedge Grass
Sedge Grass
Sedge Grass
Sedge Grass
Sedge Grass
Sedge Grass
Group IV
Marsh Edge
Marsh Edge
Marsh Edge
Marsh Edge
Sedge Grass
Sedge Grass
Group V
Marsh Edge
Tamarix
Group VI
Russian Olive
Russian Olive
Group VII

Fig. 2. Cluster diagram showing the relationships existent between 35 study sites where *Glaux maritima* was found growing. Relationships are based on species cover.

undation in the early season, the meadows are generally free of standing water by midsummer. Groundwater levels are most often at or near ground surface.

The Saline Meadow stands (Groups 2 and 3; Fig. 2) occur around the entire shoreline of the lake with the exception of the northwest corner. The soils in these meadows are seasonally wet and the communities are dominated mainly by *Distichlis spicata* (Table 2). Group 2 can be differentiated from Group 3 because of the high cover values of *Eleocharis palustris* and *Juncus balticus* in the vegetation. The presence of these two species indicates higher moisture levels in Group 2 than Group 3.

TABLE 2. Species encountered and the communities in which they occurred. Figures represent the mean cover in the groups (Fig. 1).

Species	Spike Rush	Saline Meadow 1	Saline Meadow 2	Sedge-grass	Marsh	Russian Olive	Inde-pendent
Actuca serriola	—	0.1	—	—	—	—	—
Agropyron intermedium	—	—	—	—	0.1	—	—
Agropyron repens	0.7	0.1	—	3.4	—	—	—
Agropyron riparium	—	0.1	—	0.1	—	—	—
Agropyron smithii	0.5	—	—	13.5	2.6	—	—
Agropyron subsecundum	—	—	—	—	—	53.9	—
Agrostis alba	1.6	1.1	—	12.70	3.8	—	—
Ambrosia artemisiifolia	0.3	1.3	3.3	8.2	5.6	1.3	0.1
Apocynum cannabinum	—	—	—	0.5	—	—	—
Asclepias incarnata	—	—	—	—	—	4.6	0.1
Asclepias speciosa	—	1.3	1.1	0.1	0.1	3.9	—
Asparagus officinalis	—	—	—	0.1	—	—	—
Aster brachyactis	1.1	—	—	—	—	—	—
Aster chilensis	0.6	5.8	4.9	8.0	1.3	—	—
Atriplex patula	—	1.3	0.2	—	1.3	1.3	—
Bidens frondosus	—	—	—	0.3	—	—	—
Bromus tectorum	—	—	—	—	—	45.1	22.1
Calamagrostis canadensis	—	1.2	—	3.3	—	—	—
Cardaria draba	—	—	—	—	—	43.6	—
Carex aquatilis	0.1	3.0	—	19.6	—	—	—
Carex aurea	—	—	—	0.1	—	—	—
Carex hoodii	—	0.1	—	—	—	—	—
Carex nebraskensis	—	0.4	—	0.5	0.7	—	—
Carex praegracilis	—	0.6	—	35.2	0.2	—	—
Carex rostrata	—	—	—	0.2	—	—	—
Castilleja linariaefolia	0.2	—	—	2.4	0.9	—	—
Castilleja minor	—	—	—	—	0.1	—	—
Centaurium exaltatum	0.1	—	—	0.1	—	—	—
Chenopodium album	—	—	—	0.3	—	—	—
Cirsium arvense	—	—	—	—	0.1	—	—
Cirsium undulatum	1.5	0.2	0.6	0.2	—	—	1.2
Cirsium utahense	—	—	—	—	—	24.2	—
Cordylanthus canescens	—	0.4	—	—	0.9	—	—
Crepis runcinata	0.4	1.1	11.25	16.8	1.0	—	—
Cressa truxillensis	—	—	—	—	—	—	4.1
Cyperus erythrorhizos	—	—	—	—	0.2	—	—
Descurainia sophia	—	—	—	—	—	—	0.1
Distichlis spicata	27.8	38.4	69.4	0.8	31.0	26.4	—
Elaeagnus angustifolia	0.1	0.1	—	—	0.2	99.99	—
Eleocharis palustris	65.6	16.0	0.2	13.5	1.3	—	1.5
Eleocharis rostellata	11.4	3.2	—	5.1	0.1	—	2.8
Equisetum hyemale	—	0.1	—	0.2	0.1	—	—
Equisetum kansanum	—	—	—	—	—	1.8	—
Erigeron lonchophyllus	0.1	—	—	—	—	—	—
Eupatorium maculatum	—	—	—	—	3.1	—	—
Festuca elatior	0.2	0.1	—	7.1	0.1	—	—
Glaux maritima	20.0	9.3	14.9	14.2	11.8	1.2	18.2
Glycyrrhiza lepidota	—	—	—	0.3	—	—	—
Grindelia squarrosa	—	—	—	—	—	0.1	—
Haplopappus lanceolatus	—	—	—	1.7	—	—	—
Helenium autumnale	—	1.2	—	—	—	—	—
Helianthus annuus	0.1	—	—	—	—	—	0.1
Hordeum brachyantherum	—	0.2	—	0.3	—	—	—
Hordeum jubatum	1.1	1.4	1.0	3.3	16.2	—	—
Iva axillaris	—	9.8	8.1	—	—	—	10.2
Juncus balticus	19.2	71.9	4.5	24.2	7.6	—	0.4
Juncus torreyi	—	—	—	—	0.1	—	—

Table 2 continued.

Species	Spike Rush	Saline Meadow 1	Saline Meadow 2	Sedge-Grass	Marsh	Russian Olive	Independent
Kochia scoparia	—	0.1	—	—	—	1.7	29.9
Koelaria cristata	—	0.6	—	—	—	—	—
Lactuca scariola	—	—	—	—	0.1	—	—
Lepidium montanum	—	—	—	—	—	—	3.6
Lepidium perfoliatum	—	—	0.4	—	—	0.1	0.1
Lycopus americanus	—	0.1	—	0.1	—	—	0.1
Lycopus lucidus	—	1.2	—	0.10	1.1	—	—
Medicago lupulina	—	0.2	—	—	—	—	—
Melilotus alba	—	0.2	—	3.9	—	6.9	—
Melilotus officinalis	—	—	—	0.3	—	—	—
Mentha arvensis	—	—	—	—	—	0.7	—
Muhlenbergia anserina	—	—	—	—	0.1	—	1.3
Muhlenbergia asperifolia	0.1	4.6	—	1.5	16.3	—	—
Panicum capillare	—	1.4	—	—	0.5	22.4	—
Panicum virgatum	1.8	—	—	0.2	—	—	—
Phlaris arundinacea	—	—	—	0.7	0.4	1.0	—
Plantago lanceolata	—	—	—	—	0.4	—	—
Plantago major	—	—	—	—	0.1	1.3	—
Poa nevadensis	—	0.8	—	—	—	—	1.0
Poa pratensis	—	0.5	—	0.1	—	—	—
Polygonum coccineum	1.1	—	—	—	—	—	—
Polygonum pennsylvanicum	0.1	—	—	0.2	0.1	1.2	—
Polygonum ramosissimum	0.1	—	—	—	—	—	0.4
Polypogon monspeliensis	0.1	2.5	—	—	—	—	0.7
Potentilla anserina	—	—	—	4.2	0.9	—	—
Potentilla gracilis	—	—	—	1.1	—	—	—
Puccinellia airoides	—	—	15.9	0.3	1.7	—	—
Ranunculus cymbalaria	0.9	—	0.1	3.3	1.1	—	—
Ranunculus testiculatus	—	0.1	—	—	—	—	1.3
Rumex crispus	—	0.2	—	—	—	—	—
Ruppia maritima	—	—	—	—	0.9	—	—
Salicornia rubra	—	0.2	—	—	—	—	—
Scirpus americanus	2.4	0.1	—	—	0.1	—	40.3
Scirpus pallidus	—	—	—	—	2.3	—	—
Scirpus pungens	1.0	0.4	0.4	7.1	67.6	50.0	—
Senecio hydrophyllus	—	1.0	—	1.9	—	—	—
Sisyrinchium halophilum	0.1	0.1	—	0.5	0.6	—	—
Sonchus asper	—	—	—	0.4	0.7	—	—
Sphenopholis obtusata	0.3	0.5	—	—	—	—	—
Sporobolus airoides	0.4	0.5	0.4	—	—	—	—
Suaeda depressa	—	—	4.9	—	—	—	—
Tamarix ramosissima	—	—	—	—	0.2	—	50.0
Taraxacum officinale	—	0.2	—	2.5	3.8	—	—
Tragopogon dubius	—	—	—	—	—	3.9	—
Trifolium pratense	—	—	0.3	2.0	17.5	—	—
Trifolium repens	—	—	—	20.1	0.1	—	—
Triglochin maritima	0.1	—	13.4	4.1	2.8	—	—
Verbena hastata	0.3	—	—	—	—	—	—
Veronica aquatica	—	—	—	—	—	—	3.8
Viguiera ciliata	—	5.1	—	—	—	—	—
Viola nephrophylla	—	12.2	—	—	—	—	—
Xanthocephalum sarothrae	—	—	—	—	—	—	0.8
Xanthium strumarium	0.1	—	—	—	—	—	0.1

The Russian olive communities (Group 6; Fig. 2) are scattered all around the lake but are found in small acreages. Russian olive is an introduced species that has invaded principally into the sedge-grass meadow areas. *Elaeagnus angustifolia* is the dominant overstory species, and the understory is dominated by *Scirpus pungens* and several weed species.

The grass-sedge meadows (Group 4; Fig. 2) are distributed around the lake on its north, east, and south boundaries but extend back from the marsh edge meadows toward higher and drier ground. These areas are seasonally saturated, but excess water generally has drained away by late spring. Groundwater levels are high all season in these areas. Sedges dominate the cover.

The differentiation of the cluster groups (Fig. 2) appears to be related to the moisture and salt tolerance relationships of the dominant species. All groups are either seasonally inundated part or all of the year or experience elevated levels of groundwater through the growing season. The moisture levels so close to the surface are due to ground water, springs, and seeps. The spikerush and marsh edge communities have consistently high water tables, whereas the other communities may experience lowered water tables late in summer.

The difference between the saline meadow groups (Groups 2 and 3; Fig. 2) is probably moisture and soluble salts related. Group 2 has lower salt levels and more moist soils and occupies the edge of the marsh. The stands in the group are dominated by *Distichlis spicata*, along with *Eleocharis palustris*, *Juncus balticus*, *Carex aquatilis*, and *Viola nephrophylla*. All of these species are associated with high levels of moisture in the soil. The Group 3 stands occupy a somewhat "drier", more saline habitat and are dominated by *Distichlis spicata*, *Pucinellia aeroides*, and *Triglochin maritima*. All are species adapted to the drier and more saline end of the gradient.

Sixteen soil factors were measured relative to the 35 stands studied. They are listed along with their mean and standard deviations in Table 3. The relation of these factors to the groups described in Figure 1 is shown in Table 4. Correlation analysis was conducted to assess any relationships between *Glaux maritima* cover and other habitat factors (Table 5).

An interesting relationship shown from correlation analysis is that between the grass and sedge life forms. They are negatively correlated ($p < .001$). As grass cover increases, sedge cover decreases. Several soil minerals are correlated to this relationship. Iron is positively correlated with sedges ($p < .05$), indicating that where sedge cover is high iron is also high. On the other hand, iron is negatively correlated with grasses ($p < .01$). Potassium shows an opposite pattern. Potassium is positively correlated with grasses ($p < .01$) and negatively correlated with sedges ($p < .05$). Magnesium ($p < .05$) and pH ($p < .01$) also show positive correlation to grasses, yet show no significant relationships with sedges. These relationships generally reflect the importance of a moisture gradient in vegetation patterns described above. Sedges occupy the wetter habitats.

Glaux maritima cover is uniformly distributed throughout the various groups (Fig. 2; Table 2), with the exception of the Russian olive communities. The Russian olive stands are in pastures that are subjected to irrigation throughout the growing season. The drastic decrease in *Glaux maritima* cover in the Russian olive stands was also shown in the correlation analysis, where *Glaux maritima* was negatively correlated to tree cover ($p < 0.1$).

Trees as a life form were positively correlated with potassium ($p < .05$) and phosphorus ($p < .01$). This relationship is also shown in Table 4, where the ppm for both these elements in the soil is somewhat higher in the Russian Olive communities. This

Table 3. Soil factors in sites where *Glaux maritima* is found growing, along with their means, standard deviations, and coefficients of variation.

Soil factor	Mean	Standard deviation	Coefficient of variation
P (ppm)	9.7514	6.05	0.6204
N (%)	0.33567	0.179	0.5333
Ca (ppm)	16392	20063	1.224
Mg (ppm)	1648.3	1051	0.6376
K (ppm)	554.81	406	0.7318
Na (ppm)	1252.8	891	0.7112
Fe (ppm)	57.712	54.5	0.9443
Mn (ppm)	36.820	143	3.884
Zn (ppm)	6.1794	9.81	1.588
Cu (ppm)	4.4754	2.41	0.5385
C (%)	9.9783	8.55	0.8569
Sand %	25.003	14.6	0.5839
Silt %	43.577	13.0	0.2983
Clay %	31.420	12.4	0.3947
pH	7.6134	0.386	0.5070
Soluble salts (ppm)	3008.3	2091	0.6951

Table 4. Relation of abiotic factors to groups in Figure 1. Numbers represent the means.

Soil factor	Spike Rush	Saline Meadow 1	Saline Meadow 2	Sedge-grass	Marsh	Russian Olive	Independent
P (ppm)	10.02	6.64	15.7	5.77	8.27	17.0	13.45
N (%)	0.389	0.265	0.323	0.37	0.303	0.239	0.370
Ca (ppm)	29915.0	10585.0	11872.0	10967.0	9479.0	7692.0	10399.0
Mg (ppm)	1275.6	1437.513565	2045.8	2566.7	1828.0	700.5	
K (ppm)	484.9	536.5	831.5	130.0	669.3	1132.0	750.5
Na (ppm)	1620.7	1194.2	1430.25	573.17	1186.17	391.5	1055.0
Fe (ppm)	67.85	65.74	21.35106	36.83	24.15	63.7	
Mn (ppm)	92.98	10.696	12.848	16.273	15.317	10.1	22.1
Zn (ppm)	8.492	8.532	1.62	6.217	4.743	3.23	5.0
Cu (ppm)	3.662	4.272	5.02	6.74	3.24	4.19	5.16
C (%)	15.762	6.224	12.678	4.867	6.597	10.95	9.28
Sand (%)	20.52	12.8	22.725	37.333	27.67	30.0	32.50
Silt (%)	41.50	51.2	45.55	36.67	40.67	41.5	57.5
Clay (%)	36.98	36.0	31.725	26.4	31.67	28.5	10.0
pH	7.542	7.12	7.86	7.63	7.797	8.0	7.70
Soluble salts (ppm)	3279.0	3250.0	5720.0	1264.0	2905.0	1905.0	2270.0

would undoubtedly reflect the use of commercial fertilizers on the pastures.

The cover of *Glaux maritima* was found to be positively correlated to parts per million sodium and soluble salts in the soil ($p < .05$). This finding is in agreement with those in other studies (Rozema 1975 and Rozema et al. 1978). These positive correlations indicate that as soil salts increase *Glaux maritima* cover also increases. *Glaux maritima* is known to be a halophyte (Adam 1977) and would therefore be expected to do well in sites with elevated levels of salt in the soil.

No other factors correlated significantly with *Glaux maritima* and its cover in central Utah, even though there was considerable variation in its occurrence from stand to stand. The lack of further correlations with biotic and abiotic parameters in its environment would indicate a wide tolerance in terms of habitat variability, since all factors measured showed coefficients of variation near 50% (Table 3).

Of paramount importance in the ecology of *Glaux maritima* would be moisture and salt levels in the soil. As before stated, all sites where this species occurred in any degree of importance also had high moisture levels throughout the growing season — this coming from springs, seeps, elevated water tables, and early spring runoff. Many areas are seasonally inundated. It appears that this plant is narrowly adapted to moisture conditions in its habitat. Either too much or too little water in the habitat tends to restrict its distribution. However, with its moisture requirements met and having a high tolerance for variability in other habitat factors, the relationships of this species to increasing salinity in its environment is more easily understood. As salts in the system increase, many species are not able to grow (Fig. 3), so halophytic species will have a competitive edge. Also, since many of the species in its habitat reproduce asexually, often forming large clones (Brotherson and Everson 1982), *Glaux maritima* could invade in areas where there are openings and thus compete with fewer species. This is well demonstrated in Figure 3, where concentrations of salt exceeding 2500 ppm show a corresponding 50% decline in number of species encountered in the sampling quadrats and the cover values of *Glaux maritima* show a corresponding 50% increase.

Literature Cited

Adam, P. 1977. The ecological significance of halophytes in the Devensian flora. New Phytologist 78:237–244.

Allixon, L. E. 1965. Organic carbon. Pages 1320–1345 In C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger, F. E. Clark, and R. C. Dinaure eds., Agronomy Series No. 9, Part 2. Methods of soil

Table 5. Results of correlation analyses between factors (biotic and abiotic) associated with sites where *Glaux maritima* was found growing.

Variable	Positive correlations	Negative correlations
Biotic factors		
Glaux maritima (cover)	Na (.05) soluble salts (.05)	
Trees (cover)	ppm P (.05) ppm K (.01)	sedges (.05)
Grasses (cover)	ppm Mg (.05) ppm K (.01) pH (.01)	ppm Fe (.01) sedges (.001)
Forbs (cover)	sedges (.01)	
Sedges (cover)	ppm Fe (.05)	ppm K (.05) trees (.05) grasses (.001) forbs (.01)
Monocots (cover)		ppm P (.05) % C (.05) pH (.01)
Abiotic factors		
P (ppm)	% C (.05) trees (.05)	monocots (.05)
Ca (ppm)	% C (.001)	
Mg (ppm)	grasses (.05)	% C (.05)
K (ppm)	pH (.05) trees (.01) grasses (.01)	ppm Fe (.001) sedges (.05)
Na (ppm)	soluble salts (.001) Glaux maritima (.05)	
Fe (ppm)	ppm Mn (.05) ppm Zn (.01) ppm Cu (.01) Sedges (.05)	ppm K (.001) pH (.05) soluble salts (.05) grasses (.01)
Mn (ppm)	ppm Fe (.05)	
Zn (ppm)	ppm Fe (.01) ppm Cu (.05)	
Cu (ppm)	ppm Fe (.01) ppm Zn (.05)	
C (%)	ppm P (.05).M ppm Mg (.05) ppm Ca (.001) soluble salts (.05)	monocots (.05
Sand (%)		% silt (.001) % clay (.001)
Clay (%)		% sand (.001) % silt (.05)
pH	ppm K (.05) trees (.01)	ppm Fe (.05) monocots (.01)
Soluble salts (ppm)	ppm Na (.001) % C (.05) Glaux maritima (.05)	ppm Fe (.05)

analysis — chemical and microbiological properties, American Society of Agronomy, Inc., Madison, Wisconsin.

Bouyoucos, G. J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. Journal of Agronomy 43:434–438.

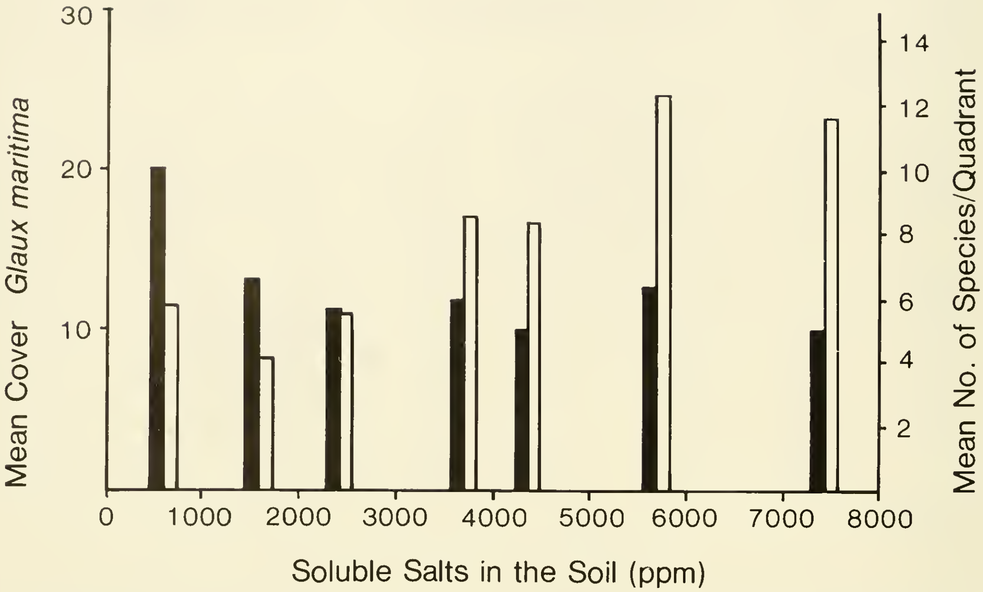

Fig. 3. Historgram showing the relationships between *Glaux maritima* cover, average number of species per quadrat, and parts per million salt in the soil. Dark bars represent average number of species per quadrat and clear bars represent *Glaux maritima* cover.

Brotherson, J. D., and W. E. Evenson. 1982. Vegetation communities surrounding Utah Lake and its bays. Utah Lake Vegetation Studies report to the Division of Wildlife Resources, State of Utah and U.S. Bureau of Reclamation, Provo, Utah 84602. 401 pp.

Christie, E. K. 1979. Ecosystem processes in semiarid grasslands II: litter production, decomposition, and nutrient dynamics. Australian Journal of Agricultural Research 30:29–42.

Cochran, W. G., and G. W. Snedecor. 1967. Statistical methods. Iowa State Univ. Press, Ames, Iowa. 593 pp.

Cronquist, A., A., H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. 1977. Intermountain flora — vascular plants of the Intermountain West, USA Vol. 1, The Monocotyledons. Columbia Univ. Press, New York. 584 pp.

Dapper, H. 1969. On the distribution of halophytes on a salty habitat in the interior of middle Europe. Experimental Plant Sociology 17:238–245.

Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. Northwest Science 33:43–66.

Grandin, M. 1973. The effect of cold and salinity on the carbohydrate concentration in the hibernacle roots of *Glaux maritima* L. Annales Des Science Naturelles 48:33–40.

——. 1981. Influence of sodium chloride and soil water saturation on development and carbohydrate, mineral element, and sodium content of *Glaux maritima*. ACTA Oecol. Plant 2(1):23–30.

Hesse, P. R. 1971. Textbook of soil chemical analysis. William Clowes and Sons, Ltd. London. 520 pp.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. of Washington Press, Seattle. 730 pp.

Holmgren, R. C., and S. F. Brewster. 1972. Distribution of organic matter reserve in a desert shrub community. U.S. Dept. Agr. Forest Serv. Res. Pap. INT-130. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Isaac, R. A., and J. D. Kerber. 1971. Atomic absorption and flame photometry: technique and uses in soil, plant, and water analysis. Pages 17–38 *in* L. M. Walsh, ed., Instrumental methods for analysis of soils and plant tissue. Soil Sci. Soc. Amer. Wis.

Jackson, M. L. 1958. Soil chemical analysis. Prentice-Hall, Inc. Englewood Cliffs, New Jersey

Jones, J. B. 1973. Soil testing in the United States. Comm. Soil Sci. Plant Anal. 4:307–322. 498 pp.

Kaesler, R. L., and J. Cairns. 1972. Cluster analysis of data from limnological surveys of the upper Potomac River. Amer. Midl. Nat. 88:56–67.

Konovov, K. E. 1978. Statistical methods of comparing the hydro thermal state of soils. Pochvovedenie 9:133–136.

Lindsay, W. H., and W. A. Norvell. 1969. Equilibrium relationships of Zn2+, Fe3+, Ca2+, and H+ with EDTA and ETPA in soil. Soil Soc. of Amer. Proc. 33:62–68.

Ludwig, J. A. 1969. Environmental interpretation of foothill grassland communities of northern Utah. Unpublished Disertation, Univ. of Utah. Salt Lake City, Utah. 100 pp.

Morden, C. 1980. Habitat and mineral composition differences of C_3 and C_4 species in Central Utah. Unpublished thesis. Dept. of Botany and Range Science. Brigham Young Univ., Provo, Utah.

Olsen, S. R., C. V. Cole, F. S. Watanabe, and L. A. Dean. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. U.S. Dept. of Agric. Circ. No. 939.

Ostler, W. K. 1980. Evaluating plant community monitoring designs: An Example from the Uinta Mountains, Utah. Unpublished Dissertation, Brigham Young Univ., Provo, Utah. 76 pp.

Ott, L. 1977. An introduction to statistical methods and data analysis. Duxbury Press, Massachusetts. 730 pp.

Rozema, J., and I. Riphagen. 1977. Physiology and ecological relevance of salt secretion by the salt gland of *Glaux maritima*. Oecologia 29:349–357.

______. 1975. An eco-physiological investigation into the salt tolerance of *Glaux maritima* L. Acta Botanica Neerlandica 24:407–416.

Rozema, J., D. A. G. Buizer, and H. E. Fabritus. 1978. Population dynamics and ecophysiological adaptations to salinity and inundation. Oikes 30:539–548.

Rozema, J., H. Gude, and G. Pollak. 1981. An ecophysiological study of the salt secretion of four halophytes. New Phytologist 89:201–217.

Rozema, J., I. Riphagen, and T. Sminia. 1977. A light and electron-microscopial study on the structure and function of the salt gland of *Glaux maritima* L. New Phytologist 79:665–671.

Russel, D. A. 1948. A laboratory manual for soil fertility students, 3d ed. Wm. Brown Co., Dubuque. 56 pp.

Ruzicka, M. 1958. Anwendung Mathematisch-Statistichae Methoden in der geobotanik (Synthetische bearbeitung von aufnahmen). Biologia, Bratisl. 13:647–661.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical taxonomy: principles and practice of numerical classification. W. H. Freeman and Co., San Francisco. 573 pp.

Stewart, G. R., J. A. Lee, and T. D. Orebamjo. 1973. Nitrogen metabolism of halophytes: II. Nitrate availability and utilization. New Phytologist 72:539–546.

Toman, M. 1976. Halophytic flora in North western Bohemia. Preslia 48:60–75.

Warner, J. H. and K. T. Harper. 1972. Understory characteristics related to site quality for aspen in Utah. Brigham Young University Science Bulletin, Biological Series, 16(2):1–20.

Welsh, S., and G. Moore. 1973. Utah plants, tracheophyta. 3d ed. Brigham Young Univ. Press, Provo, Utah. 474 pp.

EFFECT OF WESTERN WHITE PINE CONE PRODUCTION VARIABILITY ON MOUNTAIN PINE CONE BEETLE POPULATION LEVELS

Michael J. Jenkins[1]

Abstract.— Yearly variation in numbers of cones produced by western white pine was found to affect the population level of the mountain pine cone beetle. In years when cone production is moderate to heavy, beetle populations increase. Increasing beetle populations are ultimately limited by poor cone crops, which increase competition for nutrients and oviposition sites. Variability in western white pine cone production is regarded as the most important factor regulating populations of the mountain pine cone beetle.

Cone production in western white pine (*Pinus monticola* Douglas), and other conifers is typically periodic, with varying numbers of years between heavy crops (Rehfeldt et al. 1971, Franklin et al. 1974, Eis 1976). In the study by Rehfeldt et al. (1971) western white pine cone production was found to follow cycles of approximately four years. Franklin et al. (1974) found western white pine to be the most consistent cone producer of several conifers studied. They found total cone crop failure to be rare in western white pine. Puritch (1972) regarded tree metabolism, climate, and biotic agents as important factors affecting cone production.

The variability in pine cone production is extremely important in regulation of cone beetle population densities. The relationship between pine cone production and cone beetle population levels has been previously reported for eastern white pine (Henson 1964, Morgan and Mailu 1976), red pine (Mattson 1971, 1978, 1980), and pinyon pine (Forcella 1980). This study reports a similar relationship between western white pine and the mountain pine cone beetle (*Conophthorus ponderosae* Hopkins = *Conophthorus monticolae* Hopkins, Coleoptera: Scolytidae).

This study was conducted during the period 1977 through 1981 at the Sandpoint Seed Orchard, Sandpoint, Idaho. The seed orchard was established in 1960 using grafts from white pine blister-rust-resistant parent trees. It has provided an interim seed source of blister-rust-resistant planting stock for reforestation (Bingham et al. 1963). Cone production began in the early 1960s and slowly increased from year to year. Increased cone production allowed a buildup in the mountain pine cone beetle population, and by 1970 a large beetle population existed in the orchard.

Materials and Methods

Beginning in 1977, and each year thereafter, counts were made of the number of cones produced and the number attacked by beetles on each tree in the orchard. The data for 1977 were provided by the USDA Forest Service, Intermountain Forest and Range Ex-

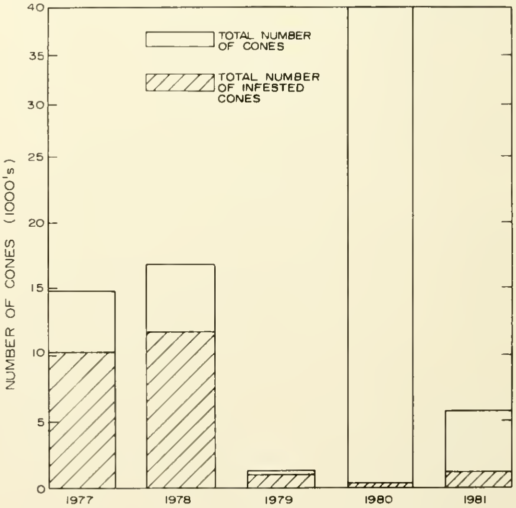

Fig. 1. The relationship between cone production in western white pine and attacks by the mountain pine cone beetle in the Sandpoint Seed Orchard, Idaho, 1977–81.

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TABLE 1. Number of trees counted, total and mean cone production, total and mean cone beetle attacks, and percent of cones attacked are shown for each of the study years.

Year	Number of trees	Cones produced		Cones attacked		Percent cones attacked
		Total	Mean	Total	Mean	
1977	591	12,651	21.41	10,136	17.15	80.12
1978	583	16,739	28.71	11,574	19.84	69.14
1979	580	830	1.43	747	1.29	90.00
1980	519	39,306	75.73	130	0.25	0.33
1981	236	5,717	24.22	305	1.29	5.33
Total		75,240	29.99	22,892	9.12	30.43

periment Station, Moscow, Idaho. Counts were made by way of binoculars, tree climbing, and a hydraulic lift truck.

RESULTS

Results of this study are shown in Table 1 and are represented graphically in Figure 1.

Moderate cone crops were produced in 1977 and in 1978, maintaining the high cone beetle population that had developed in preceding years. In 1979 cone production was very low and severe cold temperatures in the winter of 1978–79 further reduced the cone crop. Cone beetle utilization of the remaining cones was nearly 100%. A large reduction in the cone beetle population occurred due to lack of available cones for oviposition and feeding. In 1980 a bumper crop was produced, but the low cone beetle population was unable to exploit the cones to any great extent. In 1981 cone production was again low, but higher than in 1979, and the beetle population increased.

DISCUSSION

Fluctuation in current year cone numbers appears to be the most important factor regulating cone beetle population size. Previous reports on red pine (Mattson 1971, 1978, 1980), ponderosa pine (Dale and Schenk 1978), and pinyon pine (Forcella 1980) described similar relationships. Beetles can survive by initial feeding in year-old cones, but the quality of such food is reduced (Morgan and Mailu 1976). In addition, old cones cannot be utilized for oviposition.

More important than food quality is food quantity, i.e., the number of cones available in a given area. Beetle populations increased when successive moderate or heavy cone crops occurred, as in 1977 and 1978. The population was ultimately limited when cone availability was drastically decreased in 1979. In 1981 the cone beetle population had adequate cones for feeding and the beetle population was again increasing.

The intermittent production of seed by various conifers may be an adaptive mechanism decreasing losses by seed and cone insects (Henson 1964). Mattson (1978) suggested that seed and cone insects, by attacking cones during heavy crop years, remove the depressing effect of a large crop on subsequent crops, thereby enhancing future abundance of host material by reducing it at present. Feeding by seed and cone insects may be partly responsible for the periodic nature of cone production.

Cone production cycles and beetle attacks are erratic, but large crops typically suffer lower percentage losses to seed and cone insects (Schenk and Goyer 1967). Damage is greatest when small crops follow large ones, because cone beetle numbers build up when food is abundant. During years when small crops are produced, competition for food and oviposition sites causes high mortality and few new beetles are produced.

LITERATURE CITED

BINGHAM, R. T., J. W. HANOVER, H. J. HARTMAN, AND Q. W. LARSON. 1963. Western white pine experimental seed orchard established. J. Forest. 61:300–301.

DALE, J. W., AND J. A. SCHENK. 1978. Cone production and insect-caused seed losses of ponderosa pine in Idaho and adjacent Washington and Montana. Bull. Forest, Wildlife, Range Exp. Sta. 24. Univ. of Idaho, Moscow. 15 pp.

EIS, S. 1976. Association of western white pine cone crops with weather variables. Canadian J. Forest Res. 6:6–12.

FORCELLA, F. 1980. Cone predation by pinyon cone beetle (*Conophthorus edulis*): dependency on frequency and magnitude of cone production. Amer. Natur. 116:594–598.

FRANKLIN, J. F., R. CARKIN, AND J. BOOTH. 1974. Seedling habits of upperslope tree species. I. A twelve-year record of cone production. Pacific Northwest Forest Range Exp. Sta. Res. Note PNW-213. 12 pp.

HENSON, W. R. 1964. *Conophthorus coniperda* and the seed production of *Pinus strobus*. Pages 185–187 *in* Breeding pest resistant trees. Pergamon Press.

MATTSON, W. E. 1971. Relationship between cone crop size and cone damage by insects in red pine seed production areas. Canadian Entomol. 103:617–621.

______. 1978. The role of insects in the dynamics of cone production of red pine. Oecologia 33:327–349.

______. 1980. Cone resources and the ecology of the red pine cone beetle, *Conophthorus resinosae* (Coleoptera: Scolytidae). Ann. Entomol. Soc. Amer. 73:390–396.

MORGAN, F. D., AND M. MAILU. 1976. Behavior and generation dynamics of the white pine cone beetle *Conophthorus coniperda* (Schwarz) in central Wisconsin. Ann. Entomol. Soc. Amer. 69:863–871.

PURITCH, G. S. 1972. Cone production in conifers. Pacific Forest Res. Center, Canadian Forest. Serv. Infor. Rep. BC-X-65. 94 pp.

REHFELDT, G. E., A. R. STAGE, AND R. T. BINGHAM. 1971. Strobili development in western white pine: periodicity, prediction and association with weather. Forest Sci. 17:454–461.

SCHENK, J. A., AND R. A. GOYER. 1967. Cone and seed insects of western white pine in northern Idaho. Distribution and seed losses in relation to stand density. J. Forest. 65:186–187.

CONFIRMATION AND EXPANSION OF THE REPORTED DISTRIBUTION OF TWO SPECIES OF IDAHO HERPTILES

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Abstract.— The county by county distribution of the tiger salamander (*Ambystoma tigrinum*) and night snake (*Hypsiglena torquata*) in Idaho from previous reports is presented. This is augmented and expanded from recent findings.

Herptiles, especially amphibians, are often neglected in environmental surveys and biological inventories of any particular geographic area. This circumstance is magnified in several western states, like Idaho, which have a low population and a small scientific community. Generally speaking, then, portions of the published range maps for some western herptiles (e.g., Stebbins 1966) are based on limited actual field data. Instead, range maps are often constructed based on the known climatic, topographic, and habitat preferences of the species in question, coupled with known occurrences of disjunct populations and tempered with empirical wisdom. The objective of this paper is to confirm the occurrence of the tiger salamander (*Ambystoma tigrinum*) and night snake (*Hypsiglena torquata*) within the Idaho ranges indicated by Stebbins (1966), based on published reports, and augment these data with recent findings.

Methods and Materials

Our interest in the distribution of these two herptiles was aroused when specimens of each, collected out of their documented range in Idaho, were brought to us. We then reviewed the scientific literature concerning the distribution of reptiles and amphibians, as well as historical accounts of early expeditions into Idaho, to generate a county by county list of records for both species. In addition, we interviewed the lower vertebrate specialists at Treasure Valley Community College, Ontario, Oregon; College of Idaho, Caldwell; College of Southern Idaho, Twin Falls; Northwest Nazarene College, Nampa, Idaho; Idaho State University, Pocatello; and University of Idaho, Moscow; plus Idaho Department of Fish and Game personnel and several local residents interested in reptiles and amphibians.

Results and Discussion

The range for the tiger salamander in Idaho illustrated in Stebbins (1966, map 5) encompasses all or part of 30 counties in the northern and eastern thirds of the state: Bannock, Bear Lake, Benewah, Bingham, Blaine, Bonner, Bonneville, Boundary, Butte, Caribou, Cassia, Clark, Clearwater, Custer, Franklin, Fremont, Idaho, Jefferson, Jerome, Kootenai, Latah, Lemhi, Lewis, Lincoln, Madison, Minidoka, Nez Perce, Oneida, Power, Shoshone, and Teton (Fig. 1). Although Dumas (1957) and Linder and Fichter (1977) suggest that tiger salamanders are probably distributed throughout the state, with the exception of a few counties in the extreme southwest, we were only able to find published records of occurrence for 2 northern and 10 eastern counties (Table 1, Fig. 1). These two disjunct populations most likely represent two subspecies: the blotched tiger salamander (*A.t. melanostictum*) in the north and the Arizona tiger salamander (*A.t. nebulosum*) in southeast Idaho (Nussbaum et al. 1983).

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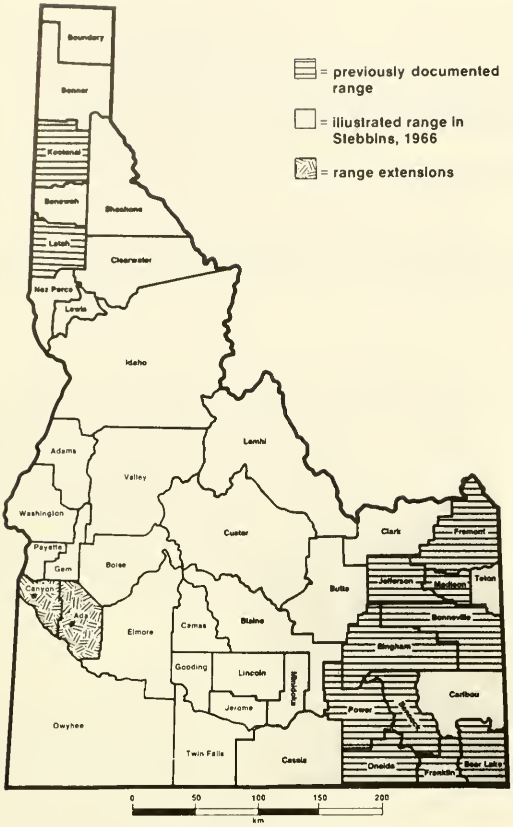
▤ = previously documented range
☐ = illustrated range in Stebbins, 1966
▨ = range extensions
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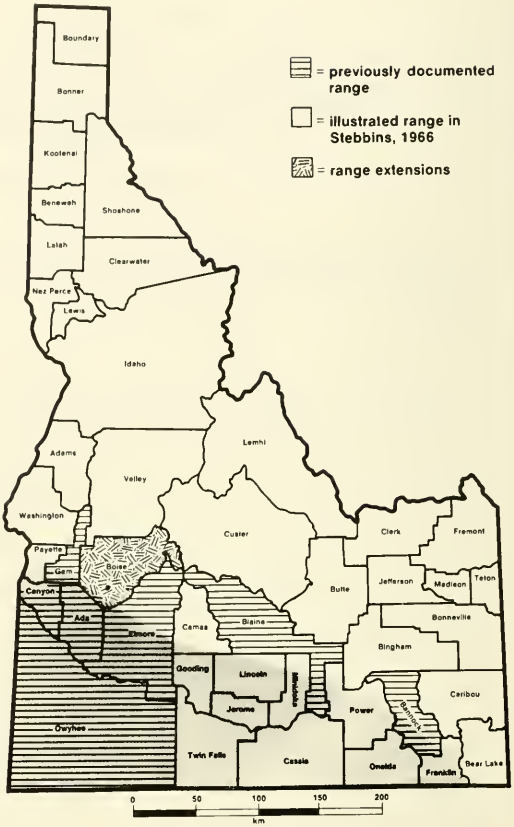
Kootenai
Benewah
Shoshone
Latah
Clearwater
Nez Perce
Lewis
Idaho
Adams
Valley
Lemhi
Washington
Payette
Gem
Boise
Custer
Clark
Fremont
Jefferson
Madison
Teton
Butte
Canyon
Ada
Elmore
Camas
Blaine
Bonneville
Bingham
Gooding
Lincoln
Minidoka
Jerome
Caribou
Power
Bannock
Owyhee
Twin Falls
Cassia
Oneida
Franklin
Bear Lake
0 50 100 150 200
km

Fig. 1. County by county range extensions for *Ambystoma tigrinum* in Idaho, compared with the previously documented range and with the illustrated Idaho range in Stebbins 1966. Black dots indicate the sites where new specimens were collected.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Custer
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Payette
Boise
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Jefferson
Madison
Teton
Canyon
Butte
Bonneville
Ada
Elmore
Camas
Blaine
Bingham
Gooding
Lincoln
Minidoka
Caribou
Jerome
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Bannock
Owyhee
Twin Falls
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Oneida
Franklin
Bear Lake
0 50 100 150 200
km

Fig. 2. County range extension for *Hypsiglena torquata* in Idaho, compared with the previously documented range and with the illustrated Idaho range in Stebbins 1966. The black dot indicates the site where the new specimen was collected.

We were unable to locate any published records of tiger salamanders in central Idaho. We have, however, documented two wild populations of tiger salamanders in southwest Idaho, precisely where Linder and Fichter (1977) predicted they would not occur (Fig. 1). The Ada County locality was 19 km SSW of Boise, and the Canyon County population was located 5.5 km E of Caldwell (R. Foote, pers. comm., 1983. Department of Biology, Treasure Valley Community College, Ontario, Oregon). We have not been able to verify whether these populations are native to the area or are introduced. Specimens collected from Ada County most closely resemble the description given by Nussbaum et al. (1983) for the subspecies *A.t. melanostictum.*

Although tiger salamanders have been collected from a number of localities in southeastern Idaho, northern Idaho, and the adjacent eastern half of Washington, no previously published records existed for the northern Great Basin areas of southwest Idaho and eastern Oregon. The records presented here for southwest Idaho extend the range of the species in Idaho about 320 km westward. Additionally, R. M. Storm (pers. comm., 1983. Department of Zoology, Oregon State University, Corvallis, Oregon) recently found tiger salamanders on Malheur National Wildlife Refuge, Harney County, in eastern Oregon. Although it is not known if this represents a natural or introduced population, this find extends the known range of tiger salamanders another 180 km westward in the northern Great Basin. Further research may reveal additional disjunct populations of the tiger salamander scattered through appropriate habitats in Idaho and elsewhere in the northern Great Basin.

TABLE 1. County by county distribution records for *Ambystoma tigrinum* in Idaho. Asterisks indicate first records for that county.

County	Reference
°Ada	Laurance and Reynolds (pers. obs., 1982)[a]
Bannock	Tanner (1941)
Bear Lake	Dunn (1940)
Bingham	Nussbaum et al. (1983)
Bonneville	Nussbaum et al. (1983)
°Canyon	Foote, R. (pers. comm., 1982. Dept. of Biology, Treasure Valley Community College, Ontario, Oregon)
Franklin	Nussbaum et al. (1983)
Fremont	Tanner (1941)
Jefferson	Nussbaum et al. (1983)
Kootenai	Dunn (1940)
Latah	Dunn (1940)
Madison	Tanner (1941)
Oneida	Dunn (1940)
Power	Nussbaum et al. (1983)

[a] Specimen in the Vertebrate Museum at Boise State University, Boise, Idaho.

TABLE 2. County by county distribution records for *Hypsiglena torquata* in Idaho. Asterisks indicate first records for that county.

County	Reference
Ada	Erwin (1925)
Bannock	Linder and Fichter (1977)
Blaine	Linder and Fichter (1977)
°Boise	Baker, C. W. (pers. comm., 1982. Dept. of Biology, Boise State University, Boise, Idaho)[a]
Canyon	Slater (1941)
Elmore	Diller and Wallace (1981)
Gem	Diller and Wallace (1981)
Owyhee	Diller and Wallace (1981)

[a] Specimen in the Vertebrate Museum at Boise State University, Boise, Idaho.

The night snake in Idaho is near the elevational extremes of its distribution in North America. Stebbins' (1966, map 175) illustrated range includes counties in the southern portion of the state: Ada, Cassia, Canyon, Elmore, Franklin, Gooding, Jerome, Lincoln, Minidoka, Oneida, and Power counties primarily (Fig. 2). The majority of the documented reports we found for this species were for five southwest counties: Ada, Canyon, Gem, Elmore, and Owyhee. The remaining reports were from Blaine (one specimen) and Bannock (two specimens) counties in southeastern Idaho (Table 2). The records from Blaine, Bannock, and Gem counties, coupled with a new report and specimen from Boise County, 22.5 km NW of Boise (C. W. Baker, pers. comm., 1982. Department of Biology, Boise State University, Boise, Idaho), suggest the Idaho range is somewhat more northerly than formerly designated, and may extend into the foothills of the northern Rocky Mountains in central Idaho.

No night snakes have been recorded from the southern tier of counties in the center of the state. The small number of night snake specimens collected elsewhere in Idaho may be the result of the secretive and nocturnal nature of this species, rather than as an actual result of a low population density or restricted distribution. Diller and Johnson (1982) report that density estimates of snakes in the Snake River Birds of Prey Area in southwest Idaho reveal that night snakes are actually the most abundant species present in that area. If this disparity between real and apparent population size exists in other areas of the state, then further censusing may fill in distributional gaps for the night snake in Idaho, particularly in the southcentral counties.

ACKNOWLEDGMENTS

We sincerely thank Dr. Charles W. Baker and Joe Maloney, whose collections of specimens truly initiated our efforts to document the ranges of *Ambystoma tigrinum* and *Hypsiglena torquata* in Idaho. Collectively we thank all the university and college biologists, state agency personnel, and interested citizens for the valuable contributions. Drs. Al Linder and Robert Stebbins reviewed the original manuscript. We thank them for their efforts.

LITERATURE CITED

DILLER, L. D., AND D. R. JOHNSON. 1982. Ecology of reptiles in the Snake River Birds of Prey Area. Contract Final Rep. USDI Bur. Land Manage., Idaho State Office. 107 pp.

DILLER, L. D., AND R. L. WALLACE. 1981. Additional distribution records and abundance of three species of snakes in southwestern Idaho. Great Basin Nat. 41:154–158.

DUNN, E. R. 1940. The races of *Ambystoma tigrinum*. Copeia 1940:154–162.

DUMAS, P. C. 1957. Introductory survey of the amphibians and reptiles of Idaho. Processed by Univ. of Idaho. 15 pp.

Erwin, R. P. 1925. Snakes in Idaho. Copeia 139:6–7.

Linder, D. D., and E. Fichter. 1977. The amphibians and reptiles of Idaho. Idaho State Univ. Press, Pocatello. 78 pp.

Nussbaum, R. A., E. D. Brodie, and R. M. Storm. 1983. The amphibians and reptiles of the Pacific Northwest. Univ. Press of Idaho, Moscow. 322 pp.

Slater, J. R. 1941. The distribution of amphibians and reptiles in Idaho. Occ. Pap. Biol., College of Puget Sound. No. 14:78–109.

Stebbins, R. C. 1966. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston i–xiv + 279 pp.

Tanner, W. W. 1941. The reptiles and amphibians of Idaho No. 1. Great Basin Nat. 2:87–97.

NATURALIZATION AND HABITAT RELATIONSHIPS OF BITTER NIGHTSHADE (*SOLANUM DULCAMARA*) IN CENTRAL UTAH

Jack D. Brotherson[1] and Kevin P. Price[2]

Abstract.— Ten plant communities containing bitter nightshade (*Solanum dulcamara*) were studied and the ecology and naturalizing relationships of bitter nightshade in central Utah area were investigated. Biotic and abiotic factors from each area were statistically analyzed. The data indicated that bitter nightshade was negatively correlated ($P < 0.01$) with perennial grass cover and positively correlated with tree overstory. Bitter nightshade reached its highest development in heavily shaded areas. No other habitat factors correlated with the presence of bitter nightshade. This lack of environmental constraints along with bitter nightshade's bright red fruits, which are readily consumed by birds, suggests possible reasons for the rapid and successful invasion of the plant into the Utah Lake area.

Bitter nightshade (*Solanum dulcamara* L.) is native to Europe, northern Africa, and eastern Asia (Crossley 1974) and was probably introduced into North America as a contaminant in crop seed used by early colonizers. Since its introduction to North America, bitter nightshade has become widespread and has invaded new areas with great success. The rapid spread of bitter nightshade may be attributed to its ornamental appeal and cultivation as an ornamental since 1561 (Crossley 1974). Also, bitter nightshade's red berries are eaten by both mammals and birds (Martin et al. 1961. Crossley (1974) writes, "The fresh berries are poisonous to most people and are fatal to rabbits, but some birds and wildlife eat them with impunity." Animals are probably the most effective method of dispersal for the plant's seeds in the wild.

Because it is an important source of aglycone solasodine, which is used in the production of steroid hormones, bitter nightshade has been intensively studied (Gatty-Kostyal et al. 1963, Gauhl 1975, Kuznetsoua and Khazanov 1973, Mathe 1974, Mathe and Mathe 1972, Mathe et al. 1975). Although several studies of bitter nightshade have focused on the environmental factors affecting the concentrations of alkaloids, few studies have been conducted concerning the naturalization and ecology of bitter nightshade. The few studies that have been conducted on bitter nightshade have been mainly in Hungary and Poland (Bernath and Tetenyu 1978, Clough et al. 1979, Gauhl 1975, Horvath et al. 1977, Nga et al. 1976). No reports are known from North America. Horvath et al. (1977) stated, "In spite of the fact that the natural occurrence of morphological and chemical taxons of this species have been analyzed in great detail, exact experiments to discover its relationship with the environment are hardly known."

The purpose of our study is to better understand the naturalization and ecology of bitter nightshade in central Utah.

Materials and Methods

Ten sites were selected depicting representative communities in central Utah in which bitter nightshade occurs (Fig. 1). At each site a 10 x 10 m study plot (0.01 ha) was established and 20 0.25 m^2 quadrats were placed at regular intervals across the plot. The study plots were delineated by a 40.0 m long cord with loops every 10 m for corners. The corners were secured by steel stakes. Variation in slope, drainage, erosion, and exposure were kept to a minimum. Density and frequency of all plant species encountered within the plots were determined from the quadrat data. Cover values were also estimated for each species as suggested by Daubenmire (1959).

Soils were sampled from the top 20 cm of the soil profile in each plot. Three samples

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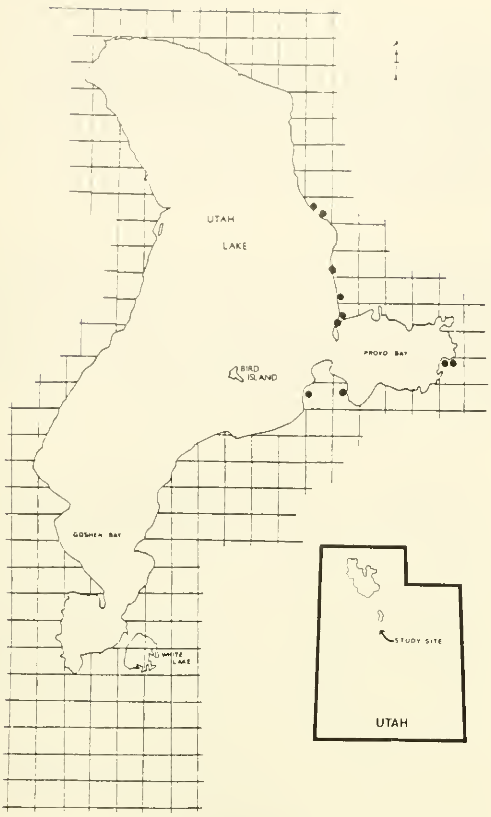

Fig. 1. Map showing the general locations of study sites in central Utah.

were taken from opposite corners and the center of each plot. Samples were pooled and analyzed for texture (Bouyoucos 1951), pH, soluble salts, and mineral content. The hydrogen ion concentration was measured with a glass electrode pH meter. Total soluble salts were determined with a Beckman electrical conductivity bridge. A paste consisting of a 1:1 g/v soil to water (distilled) mixture (Russel 1948) was used in determining pH and total soluble salts. Soil samples were also analyzed for total nitrogen (Brenner 1965), phosphorus (Olsen and Dean 1965), magnesium and calcium (Heald 1965), potassium and sodium (Pratt 1965a and Pratt 1965b), zinc, iron, copper, and manganese (Lindsay and Nowell 1969).

Cluster analysis (Sneath and Sokal 1969) was used to group the study sites which were similar with respect to species composition from the various microhabitats found within the community.

In addition to field studies, data were obtained from herbarium specimens obtained from seven college and university herbaria in Utah (Brigham Young University at Provo, University of Utah at Salt Lake City, Weber College at Ogden, Utah State University at Logan, College of Eastern Utah at Price, Dixie College at St. George, and Southern Utah State College at Cedar City). Data taken from the herbarium specimens included information on collection sites, habitat types, elevation, collection dates, and phenology. A dot map was constructed to show the distribution of bitter nightshade within the state of Utah.

The biotic and abiotic data were treated statistically by calculating the mean, standard deviation, and coefficient of variation for each factor. Simple correlation (Ott 1977) was used to determine significant relationships between percent cover of bitter nightshade and all other habitat factors. In addition, P x F (Presence x Frequency) (Anderson 1964, Curtis 1959) and Niche Breadth (Colwell and Futuyma 1971) indicies were computed for all species found in the study area to give an indication of that species importance in the community. A prevalent species list was then constructed (Warner and Harper 1972).

RESULTS AND DISCUSSION

In a 1926 floral study of Utah Lake, bitter nightshade was not listed for any of the communities studied (Cottam 1926). However, our 1979 data shows that bitter nightshade makes up 37% of the average cover in the mixed deciduous woodlands around the lake (Fig. 1). Herbarium specimen data showed that 53% of the bitter nightshade specimens collected in the state were found at elevations between 4000 and 5000 feet with a total range in elevation from 4000 to 8000 feet. The distribution map (Fig. 2) for the state of Utah shows that the plant has spread mostly in the northern portion of the state, where the major wetlands of the region are also located. The plants collected in western Juab County and in Uintah County were located at the Fish Springs Bird Refuge and Ourey Wildlife Refuge, respectively (Fig. 2).

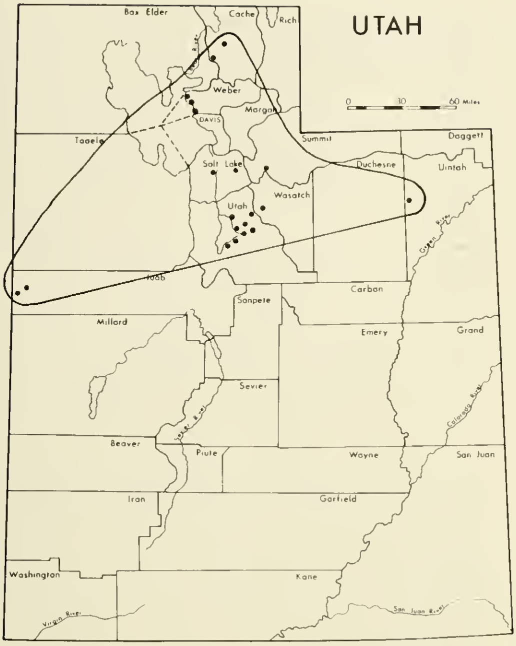

Fig. 2. Distribution of bitter nightshade in Utah based upon herbarium specimens.

Using cover data the average percent cover values for the major life forms of the communities invaded by bitter nightshade were tabulated (Table 1). As shown, total cover was very high with trees, perennial forbs and grasses making up over 90% of the ground cover. Of the 22% perennial forb cover, 89% is contributed by bitter nightshade.

Based upon a P x F Index, bitter nightshade ranked as the second most important species on the sites studied (Table 2). Bitter nightshade also had the greatest Niche Breadth of any species in the sampled community (Table 2). This would indicate that bitter nightshade is generally more adaptive than other species found growing with it.

Of the correlations between bitter nightshade cover and the biotic and abiotic factors, only the correlation between perennial grass cover and bitter nightshade cover was significant. The correlation of bitter nightshade cover to perennial grass cover gave an r value of -0.6518; the relationship was significant at the .05 level. A similar correlation between the most abundant perennial grass, quackgrass (*Agropyron repens* (L.) Beauv.), and bitter nightshade produced an r value of -0.8780, which is highly significant ($P < .001$) (Fig. 3). Quackgrass was found growing on sites that received a high incidence of sunlight, and bitter nightshade was found growing on the more shaded sites. Quackgrass apparently is more competitive than bitter nightshade on the sunny sites. It would appear that bitter nightshade is best adapted to shaded areas, although not entirely restricted to them, and quackgrass, which is less shade tolerant, does much better on the more sunny and open sites.

Most ecological studies of bitter nightshade focus on environmental factors affecting concentrations of alkaloids. Several studies deal with the effects of varying light quality and intensity on alkaloid production (Gauhl 1975, Kuznetsova 1971a, Kuznetsova 1971b, and Kuznetsova and Khagnov 1973). Gauhl (1975) for example, states that bitter nightshade exhibits great variation within the species for tolerance to varying light intensities. He also points out that plants selected from shaded habitats were damaged when exposed to high light intensities, but those selected from sunny habitats demonstrated an increase in photosynthesis and CO2 uptake. Further, Clough

Table 1. Life forms within the mixed deciduous woodland communities heavily invaded by bitter nightshade in central Utah. Figures are in percentage cover.

Biotic factors	High	Low	Mean	Standard deviation	C.V.
Total cover	100.0	99.0	99.9	0.3	0.003
Trees	81.3	45.9	62.0	12.7	0.58
Perennial forbs	41.3	1.8	23.6	13.8	0.59
Annual forbs	19.0	1.0	6.2	6.2	1.00
Perennial grasses	39.9	0.2	8.1	13.9	1.72
Annual grasses	0.3	0.1	0.1	0.1	2.50
Shrubs	0.9	0.3	0.1	0.3	2.42
Diversity	7.7	2.3	4.9	2.1	0.42
Species/Stand	24.0	5.0	13.2	6.6	0.50

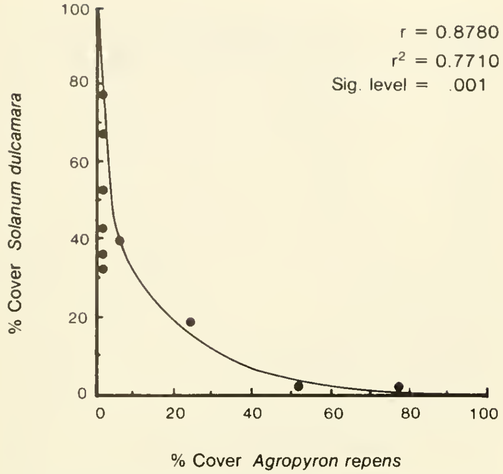

Fig. 3. Relationships existent between average percent cover of bitter nightshade and quackgrass.

et al. (1979) studied the growth performance and photosynthetic activity of bitter nightshade under a range of 12 environmental factors that simulated varying habitat conditions with respect to light intensity, moisture availability, and daily temperature amplitudes. They found no ecotypic differentiation with respect to the sun and shade environments from which the individuals were collected. All but one of the field-collected individuals was capable of successfully inhabiting a full range of light environments. We also found individuals of bitter nightshade inhabiting a full range of light environments, but it always contributed its greatest cover in the shaded areas.

Soil texture in the communities invaded by bitter nightshade (mixed deciduous woodlands) in central Utah were sandy clay loams. However, standard deviations for the percent sand, silt, and clay were highly variable, and therefore it was concluded that bitter nightshade is an opportunist that can grow and survive in a high diversity of soil textures (Table 3). Nga et al. (1976) also reported that microclimate played only a small role in the ability of bitter nightshade to inhabit a site. The soils also tended to be alkaline in nature and low in soluble salts and organic matter content (Table 3). Mineral content in the soils invaded were typical of the Utah Lake area. All measured minerals were found in sufficient quantities and were nonlimiting as far as the health and vigor of the vegetation was concerned (Table 4). Coefficients of variation (with exception of calcium) indicate a great deal of fluctuation in mineral concentrations across the sites studied.

Cluster analysis of the cover data (Fig. 4) revealed the following four groups: Group 1 consisting of sites 1, 6, 9, and 10; Group 2, sites 3 and 8; Group 3, sites 2 and 7; and Group 4, sites 4 and 5. The average percent cover of the major species found in the four groups was calculated and recorded (Table 5). As can be seen bitter nightshade is most abundant in Groups 1 and 2. These groups also have high corresponding tree cover. Groups 3 and 4 have the lowest percent of bitter nightshade and correspondingly less tree cover. It was assumed that the difference in relative cover of bitter nightshade in

Table 2. Prevalent species list for sites invaded by bitter nightshade in central Utah.

Species	P x F index	% Average frequency	% Average cover	Niche breadths
Salix amygdaloides	47.3	59.1	67.3	0.83
Solanum dulcamara	41.2	41.2	37.4	0.89
Atriplex triangularis	12.0	20.0	19.5	0.81
Populus deltoides	9.7	19.3	15.6	0.71
Agropyron repens	7.4	18.5	14.7	0.72
Conyza canadensis	3.3	6.5	12.5	0.56
Tamarix ramosissima	3.2	6.4	5.4	0.47
Salix fragilis	2.6	1.3	4.4	0.68
Cirsium arvense	2.3	4.5	3.9	0.74
Arctium minor	2.1	7.1	2.5	0.53
Xanthium stumarium	2.1	3.5	2.3	0.62
Polygonum coccineum	1.5	3.0	2.1	0.72
Lactuca serriola	1.3	4.4	1.8	0.67

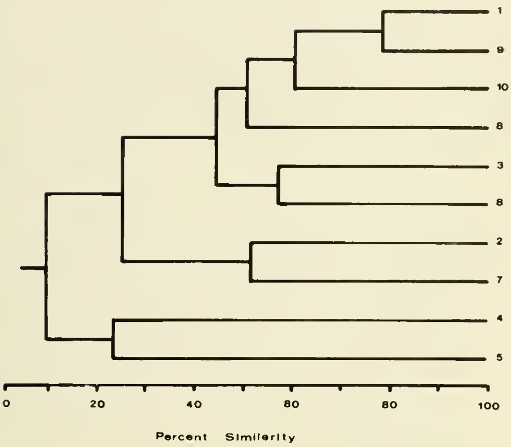

Fig. 4. Dendogram from cluster analysis showing the similarities among the 10 study sites.

Groups 1 and 2 when compared to Groups 3 and 4 was due to the high amount of tree cover and therefore less competition from perennial grass cover.

Areas of high bitter nightshade cover corresponded to areas of high overstory cover. Higher overstory generally indicates higher stem densities, and since bitter nightshade is a climbing vine, there is greater opportunity for bitter nightshade to use these stems for support. Conversely, high overstory values also indicate more shade and therefore less opportunity for the shade-intolerant grasses to compete. This should also help explain the negative relationships between the two plant types. Light intensity and extreme adaptability to varying environmental conditions seem to greatly influence the naturalization of bitter nightshade in the Utah Lake area. Light influence is also evident in the relationships represented by *Atriplex triangularis* (a shade-intolerant forb) since it increases in the understory as grass cover increases (Table 5).

We conclude that bitter nightshade naturalization is accelerated by the presence of favorable habitat (areas of high overstory cover and moist soil conditions) and a general lack of other biotic and abiotic constraints in areas of invasion. The only significant correlation of bitter nightshade cover was with perennial grasses, more specifically quackgrass. It is felt that the negative correlation between the two plants is best attributed to the fact that grasses are generally more drought tolerant and less shade tolerant than are forbs (Yake and Brotherson 1979). Also, the highly rhizomatous nature of quackgrass makes it very competitive once established.

TABLE 3. Measured soil factors of communities invaded by bitter nightshade along with their means, standard deviations, and coef. of variations.

Abiotic factors	High	Low	Mean	Standard deviation	C.V.
Sand	94.0	14.0	54.7	31.4	0.57
Silt	59.0	2.0	22.3	20.0	0.90
Clay	74.0	2.0	22.8	20.9	0.92
Fines (silt, clay)	86.0	4.0	45.1	31.7	0.70
Soluble salts (ppm)	3959.0	399.0	2240.0	1548.8	0.69
pH	8.5	7.5	8.0	0.4	0.04
Carbon	12.1	1.3	6.7	2.9	0.43

TABLE 4. Soil chemical factors from the communities invaded by bitter nightshade along with their means, standard deviations, and coefficients of variations.

Abiotic factors	High	Low	Mean	Standard deviation	C.V.
Phosphorous (ppm)	81.6	8.4	24.9	22.1	0.89
Nitrogen (ppm)	2480.0	190.0	1058.7	710.4	0.67
Calcium (ppm)	14800.0	4275.0	9852.5	2865.7	0.29
Magnesium (ppm)	2850.0	204.0	1038.9	826.2	0.80
Potassium (ppm)	270.0	39.0	166.7	144.0	0.86
Sodium (ppm)	1625.0	98.0	522.8	455.3	0.85
Iron (ppm)	210.0	7.6	80.6	65.1	0.81
Manganese (ppm)	13.2	2.3	7.9	4.0	0.50
Zinc (ppm)	76.8	0.9	14.0	22.7	1.62
Copper (ppm)	39.4	0.2	5.1	12.2	2.39

Table 5. Average cover by species within the four groups designated in the cluster analysis.

	Groups from cluster analysis			
	1	2	3	4
Acer negundo	0.0	0.0	0.4	0.0
Agropyron repens	19.6	0.0	49.8	28.4
Ambrosia artemisifolia	0.0	0.1	0.0	2.8
Arctium minus	0.0	1.6	0.1	25.2
Atriplex triangularis	0.1	0.5	22.7	39.1
Cardaria draba	0.0	0.0	1.4	1.3
Cirsium arvense	0.0	7.8	0.0	3.5
Convolvulus sepium	0.7	0.4	0.0	0.0
Conyza canadensis	0.0	17.4	4.0	0.4
Distichlis spicata var. *stricta*	0.0	0.0	9.0	0.0
Fraxinus pennsylvanica	0.0	0.0	0.0	7.9
Galium trifidum	0.0	0.0	1.3	0.0
Lactucca serriola	0.0	0.0	4.5	2.8
Lycopus lucidus	0.2	3.0	0.0	0.0
Mulhenbergia asperifolia	0.0	0.0	1.3	0.0
Nepeta cataria	0.0	0.0	0.0	1.3
Phalaris arundinacea	0.0	0.0	2.7	0.4
Polygonum coccineum	1.5	6.2	0.0	1.3
Populus deltiodes	7.3	43.2	4.5	35.2
Rumex sp.	1.2	0.0	0.0	0.0
Salix amygdaliodes	95.8	65.9	79.1	0.0
Salix exigua	0.0	0.0	0.4	1.4
Salix fagilis	0.0	0.0	0.0	73.6
Solanum dulcamara	35.5	45.4	10.9	20.8
Sonchus asper	0.0	0.0	0.0	4.7
Tamarix ramosissima	0.4	0.4	18.5	0.0
Urtica dioica	0.8	8.5	0.0	0.0
Xanthium strumarium	0.9	6.0	0.1	0.8

LITERATURE CITED

Anderson, O. 1964. The phytosociology of dry lime prairies of Wisconsin. Unpublished dissertation, Univ. of Wisconsin.

Bernath, J., and P. Tetenyi. 1978. Ecological factors adaptability relationship of steroid alkaloid production based on investigation of 2 species, *Solanum-laciniatum* and *Solanum-dulcamara* Acta Botanica Academiae Scientiarum Hungaricae 24:41–56.

Bouyoucos, G. J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. Agronomy J. 43:434–438.

Brenner, J. M. 1965. Total nitrogen. Pages 1149–1178 *In* C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger, F. E. Clarck, eds., Methods of soil analysis, chemical and microbiological properties. Number 9, part 2. American Society of Agronomy, Inc., Madison, Wisconsin. 801 pp.

Clough, J. M., J. A. Teeri, and R. S. Alberte. 1979. Photosynthetic adaption of *Solanum dulcamara* L. to sun and shade environments: I. A comparison of sun and shade population. Oecologia 38:13–22.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Cottam, W. P. 1926. An ecological study of the flora of Utah Lake, Utah. Unpublished Dissertation, Univ. of Chicago. 46 pp.

Crossley, J. A. 1974. Seeds of woody plants in the United States. USDA For. Ser. Agric. Handbook No. 450. 779 pp.

Curtis, J. T. 1959. The vegetation of Wisconsin. Univ. of Wisconsin Press, Madison, Wisconsin. 657 pp.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43–46.

Gatty-Kostyal, M., B. Adamczyk, M. Kostolowska, and L. Markiewica. 1963. Physiology of the deadly nightshade. Dissertationes Pharmaceutica et Pharmacologicae 15:215–234.

Gauhl, E. 1975. Photosynthetic response to varying light intensity in ecotypes of *Solanum dulcamara* L. from shaded to exposed habitats. Oecologia 22:375–381.

Heald, W. R. 1965. Calcium and magnesium. Pages: 999–1010. *in*: C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger, F. E. Clarck, eds., Methods of soil analysis, chemical and microbiological properties. Number 9, Part 2. American Society of Agronomy, Inc., Madison, Wisconsin. 801 pp.

Horvath, I., J. Bernath, and P. Tetenyi. 1977. Effect of the spectral composition of light on dry matter production in *Solanum dulcamara* L. ecotypes of different origin. Acta Agronomica Academiae Scientiarum Hungaricae 26:346–354.

Kuznetsova, G. K. 1971a. Quality of light and its effect on photosynthesis and alkaloid contents in nightshade and groundsel. Fiziologiys Rastenii 18:18–22.

———. 1971b. Quality of light and its effect on photosynthesis and alkaloid contents in nightshade and groundsel. Soviet Plant Physiology 18:13–16.

Kuznetsova, G. K., and V. S. Khazanov. 1973. Spectral effectiveness of some alkaloid-bearing plants during adaption to light of different quality. Fiziologiya Rastenii 20:554–557.

Lindsay, W. L., and W. A. Norvell. 1969. Development of a DTPA micronutrient soil test: equilibrium relationships of Zn2+, Fe3+, Ca2+II, H+ with EDTA and DTPA in soil. Page 84 *in* Agronomy Abstracts. Soil Sci. Soc. Amer. Proc. 33:62–68.

Martin, A. C., H. S. Zim, and A. L. Nelson. 1961. American wildlife and plants, a guide to wildlife food habitat. Dover Publications, Inc., New York. 415 pp.

Mathe, I., Jr. 1974. Contributions to the study of alkaloid content in different organs (leaf, stem, fruit, root) of *Solanum dulcamara*. Botanikai Kozlemenyek 61:133–139.

Mathe, I., Jr., G. Toth, S. Vajda, and I. Mathe. 1975. Studies on the effects of ecological factors on *Solanum dulcamara*. Acta Gronomia Academiae Scientiarum Hungaricae 24:325–334.

Mathe, I., Sr., and I. Mathe, Jr. 1972. The alkaloid content of *Solanum dulcamara* L. populations in Hungary. Herba Hungarica 11:5–12.

Nga, V. H., J. Bernath, and P. Tetenyi. 1976. Response of a *Solanum dulcamara* population to ecological factors. Part 1. Fittedness and instability of morphophenological features. Herba Hungarica 15:31–44.

Olsen, S. R., and L. A. Dean. 1965. Phosphorus. Pages 1035–1099 *in* C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger, and F. E. Clarck, eds., Methods of soil analysis chemistry, chemical and microbiological properties. Number 9, part 2. American Society of Agronomy, Inc., Madison, Wisconsin. 801 pp.

Ott, L. 1977. An introduction to statistical methods and data analysis. Duxbury Press, Massachusetts. 730 pp.

Pratt, P. F. 1965a. Potassium. Pages 1022–1249 *in* C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger, and F. E. Clarck eds., Methods of soil analysis, chemical and microbiological properties. Number 9, part 2. American Society of Agronomy, Inc., Madison, Wisconsin. 801 pp.

______. 1965b. Sodium. Pages 1031–1039 *in* C. A. Black, D. D. Evans, J. L. White, L. E. Ensminger, and F. E. Clarck, eds., Methods of soil analysis, chemical and microbiological properties. Number 9, part 2. American Society of Agronomy, Inc., Madison, Wisconsin. 801 pp.

Russel, D. A. 1948. A laboratory manual for soil fertility students, 3d ed., William Brown Company, Dubuque, Iowa. 56 pp.

Sneath, P. H. A., and R. R. Sokel. 1973. Numerical taxonomy — the principle and practice of numerical classification. W. H. Freeman and Company, San Francisco, California. 573 pp.

Warner, J. H., and K. T. Harper. 1972. Understory characteristics related to site quality for aspen in Utah. BYU Sci. Bull., Biol. Ser., 16:1–20.

Yake, S., and J. D. Brotherson. 1979. Differentiation of serviceberry habitats in the Wasatch Mountains of Utah. J. of Range Manag. 32:379–383.

DISTRIBUTION OF THE SHOSHONE SCULPIN (*COTTUS GREENEI*: COTTIDAE) IN THE HAGERMAN VALLEY OF SOUTH CENTRAL IDAHO

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Patrick J. Connolly[1] and G. B. Beckham[2]

ABSTRACT.— *Cottus greenei*, a potentially threatened species endemic to Idaho, was collected from 49 localities in 25 springs/streams in south central Idaho. Most localities were along the north bank of the Snake River in waters of the Thousand Springs formation, Gooding County. One population was found in a spring in the main Snake River. Another sculpin, *Cottus bairdi*, was collected with *C. greenei* at 23 locations in 16 springs/streams. Confusion concerning the type locality of *Cottus greenei* is discussed.

The Shoshone sculpin, *Cottus greenei* (Gilbert and Culver 1898), has the most restricted distribution of any native fish in Idaho except the endemic fishes of Bear Lake. Until recently, the species was known to occur only in three streams (Riley, Sand Springs, and Billingsley creeks) in the Thousand Springs area of the Hagerman Valley of south central Idaho (Simpson and Wallace 1978). Wallace (1980) reported *Cottus greenei* from one additional stream in the area and noted the possibility of its occurrence in the main Snake River. The U.S. Fish and Wildlife Service initiated a status review of *C. greenei* in 1980 because of its restricted distribution and impending development of waters in the area. By that time, the species was known to occur in at least 10 streams and springs in the Thousand Springs formation (Williams 1980). During 1981 we made over 130 collections from about 100 localities in the area to define the distribution of the Shoshone sculpin more clearly. This report on the distribution of *Cottus greenei* is a segment of a larger study to determine the distribution, abundance, habitat preferences, and life history of this potentially threatened fish species in Idaho. Specific locations of all populations of *Cottus greenei* collected by us and sampling sites where *C. greenei* were not found are on file at the University of Idaho and Idaho State University.

TAXONOMY AND TYPE LOCALITY

The Shoshone sculpin was named and described as *Uranidea greenei* by Gilbert and Culver (1898:1965). *Uranidea* was later synonymized with *Cottus* (Jordan et al. 1930). There has been some confusion concerning the location of the type locality of *C. greenei*. The original description was based on specimens collected in 1894 (Jordan and Evermann 1898). The type locality was listed as "Thousand Springs, Snake River, Idaho, near mouth of Salmon Fall River." Salmon Fall River (now referred to as Salmon Falls Creek) enters the Snake River from the south, nearly opposite Thousand Springs. Thus, Salmon Falls Creek might be considered the type locality. The expedition on which the type of *C. greenei* was collected was different from that reported by Gilbert and Evermann (1894) (Robert R. Miller, pers. comm.). Therefore, the type locality of *Cottus greenei* is Thousand Springs, Gooding County, Idaho, and not Salmon Falls Creek, Twin Falls County.

One specimen of *Cottus greenei* housed in the fish collection of the Museum of Zoology, University of Michigan (UMMZ 157055) is labeled as being collected from Salmon Falls Creek in 1948 by James Simpson of the Idaho Department of Fish and Game. Mr. Simpson told us he never found *C. greenei* on the

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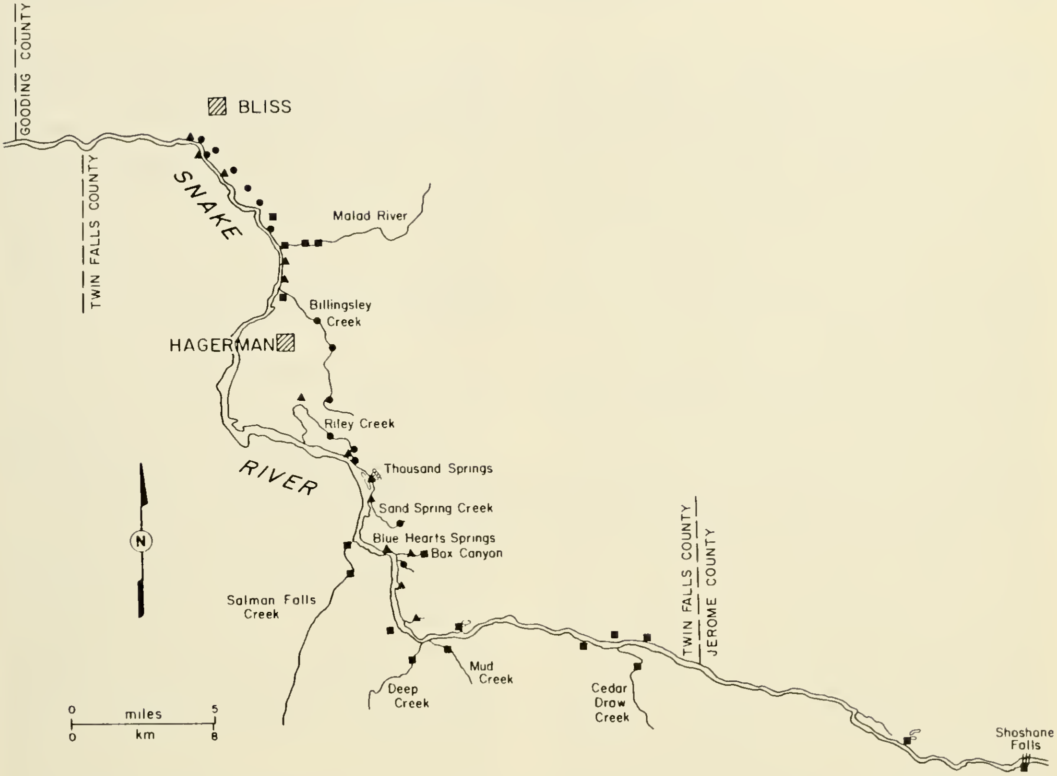
GOODING COUNTY
TWIN FALLS COUNTY
BLISS
SNAKE
Malad River
Billingsley Creek
HAGERMAN
Riley Creek
Thousand Springs
RIVER
Sand Spring Creek
Blue Hearts Springs
Box Canyon
N
Salmon Falls Creek
Deep Creek
Mud Creek
Cedar Draw Creek
TWIN FALLS COUNTY
JEROME COUNTY
Shoshone Falls
0 miles 5
0 km 8

Fig. 1. Distribution of Shoshone sculpin (*Cottus greenei*) and mottled sculpin (*C. bairdi*) in the Hagerman Valley area of south central Idaho. Not all localities are shown.

south side of the Snake River and does not remember ever collecting it in Salmon Falls Creek (James Simpson, pers. comm.). This same information was transmitted to R. M. Bailey when Simpson's Idaho fish collections were sent to Michigan in April 1948 (Robert R. Miller, pers. comm.). We made three separate collections in lower Salmon Falls Creek, one very near the place where Mr. Simpson collected in 1948, and found only *Cottus bairdi*. Therefore, we believe that the locality data on that specimen, UMMZ 157055, are incorrect and that *Cottus greenei* does not occur in Salmon Falls Creek.

Methods

We used D.C. and A.C. electrofishing gear and dip nets to collect sculpins from most localities. Scuba surveys were made in deep pools of tributary streams and in areas of the main Snake River. Divers collected sculpin with hand-operated slurp guns. When possible, sculpin were identified and released at the place of capture. Some samples were preserved in 10% formalin to fulfill other objectives of the study. All preserved specimens will be retained in the fish collections at the University of Idaho and Idaho State University.

Results and Discussion

Cottus greenei was found at 49 locations in 25 springs/streams in the Hagerman Valley (Fig. 1). With two exceptions, *C. greenei* occurred only in Gooding County. Most sites were within the Thousand Springs formation along the north bank of the Snake River between River Miles (RM) 565.8 and 590.5. We found only two localities containing *C. greenei* on the south side of the Snake River in Twin Falls County. An unnamed spring flowing into the Snake River at RM 566.6 contained a very small population of Shoshone sculpin. At RM 588.3, a few *C. greenei* were found in the outflow from the private fish hatchery. Their water supply is collected from Box Canyon Springs, immediately across the Snake River, and piped to the south bank where the hatchery is located. Apparently, some individual sculpin have been transported across the Snake River with the water that is diverted to this hatchery. The most upstream collection came from Briggs Springs at RM 590.5. There are many additional springs entering the Snake River above this site, but intensive sampling and an analysis of existing collections of sculpins from these areas revealed only the mottled sculpin, *Cottus bairdi*.

The mottled sculpin was found throughout the area and was the only species of sculpin found in the streams entering the Snake River from the south. *C. bairdi* was found sympatrically with *C. greenei* at 23 localities in 16 streams/springs in the area. Other fish species collected in the area included rainbow trout (*Salmo gairdneri*), brown trout (*Salmo trutta*), longnose dace (*Rhinichthys cataractae*), speckled dace (*R. osculus*), northern squawfish (*Ptychocheilus oregonensis*), redside shiner (*Richardsonius balteatus*), chiselmouth (*Acrocheilus alutaceus*), peamouth chub (*Mylocheilus caurinus*), largescale sucker (*Catostomus macrocheilus*), largemouth bass (*Micropterus salmoides*), and bluegill (*Lepomis macrochirus*). Rainbow trout, brown trout, longnose dace, and mottled sculpin were found sympatrically with the shoshone sculpin except at two localities. At Blue Hearts Springs in the Snake River, redside shiners, largescale suckers, and largemouth bass were also collected. Redside shiners were collected with *C. greenei* in Upper Sand Springs Creek. *C. greenei* was not found in the Malad River (four sampling locations), Salmon Falls Creek (three sites), or Deep, Mud, and Cedar Draw creeks.

Most locations sampled apparently contain small populations of *C. greenei*, perhaps only a few dozen to a few hundred individuals. At least three sites, however, support populations of thousands of Shoshone sculpin. Two of these sites, Box Canyon and Blue Hearts Springs, are entirely or partially on public lands administered by the Bureau of Land Management. The third site, Sand Springs Creek, is under private ownership, as are most of the springs supporting smaller populations of *C. greenei*. Riley creek, a stream containing a fairly large population of *C. greenei*, flows through state and federal fish cultural stations and a state wildlife management area. Most populations in this stream, however, are located in the various springs feeding the creek and in the hatchery raceways. We found no *C. greenei* in Riley Creek below the wildlife management area.

ACKNOWLEDGMENTS

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LITERATURE CITED

Gilbert, C. H., and B. W. Evermann. 1984. A report upon investigations in the Columbia River basin, with descriptions of four new species of fishes. Bull. U.S. Fish. Comm., 14:169–207.

Gilbert, C. H., D. S. Jordan, and B. W. Evermann, Culver. 1898. *Uranidea greenei*, new species. Page 1965 *in* D. S. Jordan and B. W. Evermann, The fishes of North and Middle America. Bull. U.S. Nat. Mus. 47(2):1241–2183.

Jordan, D. S., B. W. Evermann, and H. W. Clark. 1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. Appendix X, Report of the U.S. Commissioner of Fisheries for 1928, part 2:LV + 670 pp.

Simpson, J. C., and R. L. Wallace. 1978. Fishes of Idaho. Univ. Press of Idaho, Moscow. 237 p.

Wallace, R. L. 1980. *Cottus greenei* (Gilbert and Culver), Shoshone Sculpin. Page 813 *in* D. S. Lee et al., Atlas of North American freshwater fishes. North Carolina State Mus. Nat. Hist., Raleigh. i–x + 854 pp.

Williams, J. D. 1980. Endangered and threatened wildlife and plants: review of the status of the Shoshone Sculpin. Federal Register, vol. 45(60):19858.

STANDING CROPS AND DYNAMICS OF PHYTOMASS AND MINERALS IN TWO SALT DESERT SHRUB COMMUNITIES

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Abstract.— Of two salt desert shrub communities studied in Curlew Valley, Utah, the *Atriplex confertifolia*-dominated community had 15% greater total midsummer phytomass than the *Ceratoides lanata* community. The larger *Atriplex* shrubs contained much more woody tissue for support of photosynthetic tissues than did *Ceratoides*. *Atriplex* aboveground phytomass and litter were about twice those of *Ceratoides*. *Ceratoides* litter was generally fine and easily decomposable, but *Atriplex* litter contained about equal proportions of coarse, resistant woody tissues and fine, easily decomposable material. *Atriplex* root phytomass was 1.3 times that of *Ceratoides* at the 2–30 cm depth, but at depths below 30 cm, *Ceratoides* exhibited up to three times greater root phytomass and had 23% more root mass overall.

Net aboveground community primary production was estimated to be about one-third greater in the *Atriplex* than *Ceratoides* community. Turnover times for readily decomposable aboveground litter were quite similar, but, because *Atriplex* produced coarser litter, its overall rate was somewhat slower than that of *Ceratoides*.

Analyses of selected minerals in plant parts, litter, and soil revealed that about 90% of the mineral capital is in the soil, mostly within organic matter. Nearly equivalent pools of mineral elements were found in the two communities, except for greater Na in the *Atriplex* community.

Primarily because of relatively low productivities, insignificant nutrient losses by leaching, and slow losses due to biological export, primary production (Caldwell 1975) and nutrient cycling processes (West 1981) of arid grazing lands have received little basic study. Disturbance of desert vegetation is followed by slow recovery. If soil erosion is great, nearly permanent damage to site potential can occur during periods of diminished vegetation. Knowledge of ecosystem structure will aid interpretations of and decisions for managing these areas.

In the interests of providing data for comparison purposes, we report the following study of standing crops and dynamics of phytomass and selected mineral elements in communities dominated by nearly pure stands of *Atriplex confertifolia* (Torr. & Frem.) Wats. (shadscale) and *Ceratoides lanata* (Pursh.) J. T. Howell (winterfat), two major, perennial species of the salt desert shrub type (West 1983) in the intermontane basins of the interior western United States. Estimates of net aboveground primary productivity and turnover rates of litter are made for both communities.

Ceratoides is more palatable to livestock and has been widely replaced by the less palatable *Atriplex confertifolia* or annual weeds (West 1982). We wished to compare production and nutrient-cycling processes on sites dominated by perennial species to anticipate whether further losses of *Ceratoides* dominance had unfavorable implications from primary production and nutrient-cycling viewpoints.

METHODS

Plant, litter, and soil samples were collected in Curlew Valley of northwestern Utah (41°52′N, 113°5′W). The sites selected were on nearly level, lacustrine soils covered by pluvial Lake Bonneville prior to about 7000 years ago (Eardley et al. 1957). The soil profiles of both sites were classified as belonging to the fine silty mesic family of Xerollic Calciorthids, Thiokol Series (A. R. Southard, pers. comm.) and were 0.8 km apart on the 1350 m contour. Previous investigators of soil chemical (Gates et al. 1956) and physical characteristics (Mitchell et al. 1965) had concluded that the soils under *Atriplex* and

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Ceratoides in this area did not differ in a statistically significant sense.

The vegetation was composed of nearly monospecific stands of the two dominant plants, *Atriplex confertifolia* and *Ceratoides lanata* (see Mitchell et al. 1965). Total higher plant cover (line intercept method) averaged 22% in the *Atriplex* and 20% in the *Ceratoides* community. *Ceratoides* plants are small half-shrubs quite evenly dispersed, whereas *Atriplex* plants are true shrubs from 5 to 20 times larger and less uniformly distributed (West and Baasher 1968). The area had been used by livestock since at least the 1870s. Because open water is at least 6 km distant, most of the livestock use was in winter by sheep. This comparatively light use has apparently allowed the more palatable species to persist in pure stands. Plots used in this study were fenced in 1967 with sheep-, cattle-, and rabbit-proof netting.

Each community was subdivided into four major components: shoots, roots, litter, and soil. A single annual sampling of each compartment was made in late July or early August of 1968, 1969, and 1970. This sampling followed the period of maximum growth of the shrubs and water-stress-induced drop of ephemeral leaves (West and Gasto 1978). Aboveground phytomass (living + standing dead plants and litter) estimates were made by harvesting plants from randomly selected 1- and 4-m^2 plots in *Ceratoides*- and *Atriplex*-dominated vegetation, respectively. Quadrat dimensions and numbers were predetermined to yield phytomass estimates within 15% of the true mean ($P \leq 0.1$). Plants were clipped at ground level and separated from adhering soil and litter.

Aboveground net primary community production was estimated by a technique using the ratio between the oven dry masses of old and new growth (Whittaker 1961) of 40 individual plants of each species. Plant numbers were predetermined to estimate this ratio within 10% of the true mean ($P \leq 0.1$).

Litter was collected from the total area of each plot after removal of aboveground plant parts. In *Atriplex* plots, the litter could be divided into two classes, a coarse fraction that was resistant to decay and composed of woody material such as dead stem bases, and a fine, easily decomposable fraction of leaves and finer stem material. Surface soil particles were removed by shaking the litter on a 1.6-mm sieve, followed by washing and flotation. The *Ceratoides* litter was virtually all of fine composition, so that fractionation was not necessary. Distinctly standing dead material was included in the litter fraction. Woody, aboveground portions of shrubs with distinctly live tissue were included in the shoot fraction. Root phytomass and soil bulk density values were determined from randomly placed 8.4-cm-diameter core samples taken with a bucket auger from the aboveground biomass sampling plots, at depth increments of 2–30, 30–60, and 60–90 cm. This sampling depth included 98% of the root mass (Gasto 1969).

Roots were partially separated from soil using a 1.6-mm sieve, followed by washing and flotation.

Old shoot growth, new shoot growth, root mass, and litter were dried with forced air at 60 C for 48 hr and ground to pass a 40-mesh sieve. Samples were analyzed for total N by semimicro Kjeldahl techniques. To determine P, K, Na, Ca, and Mg content, a 1.0 g sample was digested for 2 hr with 16 ml HNO_3 + 2.4 ml $HClO_3$ + 1.6 ml H_2SO_4, after which it was cooled, filtered, and diluted to an appropriate volume. Phosphorus was determined colorimetrically as phospho-vanado-molybdate and other elements were measured by atomic absorption spectrophotometry. Only soil organic carbon is included here since total carbon budgets of these ecosystems had been previously considered by Caldwell et al. (1977).

The soil organic carbon was determined by wet combustion in an excess of potassium dichromate solution. Excess dichromate was reduced by addition of ferrous ammonium sulfate solution, which in turn was titrated with standardized potassium permanganate solution. The difference between the amount of standardized potassium permanganate used in titrating blanks and soil samples served as the basis for calculation of organic carbon. Since soil samples contained appreciable quantities of carbonate and chloride salts, concentrated sulfuric acid containing 25 g of silver sulfate per pound was used to drive off inorganic carbonates and prevent interference of chlorides by precipitating with the silver ion (Jackson 1958).

The soil separated from each of the root mass samples was air dried prior to chemical analysis. Total N was determined by the Kjeldahl procedure. Soil P was extracted by .5 *N* $NaHCO_3$ and determined by the phosphovanado-molybdate method, and other minerals were determined by atomic absorption on a HNO_3-HCO_3 (3:1) digestion.

Total soluble salt content of soil was determined by measuring resistance of the saturated soil paste and converting the temperature-adjusted values according to method 5 (U.S. Salinity Laboratory 1954).

Results and Discussion

Phytomass

Total midsummer phytomass, as well as the amounts in most compartments, significantly differed between communities (Table 1). Total plant and litter weights in the *Atriplex* community were about 15% greater than those found in the *Ceratoides* community. *Atriplex* showed about 60% greater total shoot phytomass than *Ceratoides*. The *Atriplex* litter phytomass fractions were over twice as great as that of the *Ceratoides*-dominated community. It is particularly significant that the current year's aboveground growth of *Atriplex* was about 20% greater than that of *Ceratoides*. Not all this new growth in *Atriplex* is photosynthetic. Caldwell et al. (1977) reported about 19% of the new shoot growth fractions of this plant to be nonphotosynthetic. Much less (about 10%) was nonphotosynthetic in *Ceratoides*. A principal difference between the aboveground phytomasses of *Atriplex* and *Ceratoides* communities appeared to be in the woody nature of the former. New growth in *Atriplex* occurs on old, woody stems, but much of the new growth of *Ceratoides* originates from a woody base, there being no hard wood in the form found in Curlew Valley. The woody, spiny nature of *Atriplex* makes it comparatively more resistant to browsing than is *Ceratoides* (Gasto 1969).

Table 1. Midsummer phytomass (oven-dry g m^{-2}) in *Atriplex confertifolia* and *Ceratoides lanata*-dominated communities, by compartments, Curlew Valley, Utah. Average of 1968, 1969, and 1970 midsummer samples ± 90% confidence intervals.

Compartment	Depth	Community type *Atriplex*	 *Ceratoides*
	cm	g m^{-2}	
Shoots			
New growth		84 ± 11	70 ± 13
Old growth		333 ± 25	172 ± 22
Total shoot phytomass		417 ± 36	241 ± 35
Roots[1]	0–30	945 ± 62	721 ± 69
	30–60	292 ± 35	668 ± 42
	60–90	76 ± 9	218 ± 30
Total root phytomass	0–90	1,313 ± 76	1,607 ± 90
Litter			
Coarse		446 ± 20	–
Fine		403 ± 26	400 ± 26
Total litter weight		849 ± 36	400 ± 26
Total plant and litter weight		2,579 ± 141	2,249 ± 119

[1] Estimate includes root litter

Only in total belowground phytomass did the *Ceratoides* system exceed *Atriplex*. *Atriplex* had somewhat more root mass in the upper 30 cm of the soil profile, but only 42% as much as *Ceratoides* was found below 30 cm.

The distribution of root biomass was closely related to soil-textural conditions and total soluble salt distribution in the two soil profiles (Fig. 1). The *Atriplex*-dominated site had higher clay content in the upper part of its soil profile. This soil has a slower infiltration rate and under equal rainfall wets to shallower depths than the *Ceratoides* soil (Gasto 1969).

The greater woodiness and concentration of roots of *Atriplex* closer to the soil surface contrasts with less woodiness and continuance of high densities of *Ceratoides* roots to greater depths. The two species thus had tissue concentrations in somewhat different microenvironments both above- and belowground. Both species had very high root:shoot ratios, also typical of dominants in cold-winter temperate deserts elsewhere (Rodin and Basilevich 1967). Brewster (1968) and Wagner (1980) have speculated that the high proportion of roots is related to most of the soil moisture coming from winter snowmelt. Cold to cool season precipitation is the only input that normally infiltrates to great enough depths to escape evaporation in such environments (Caldwell et al. 1977). Arrested

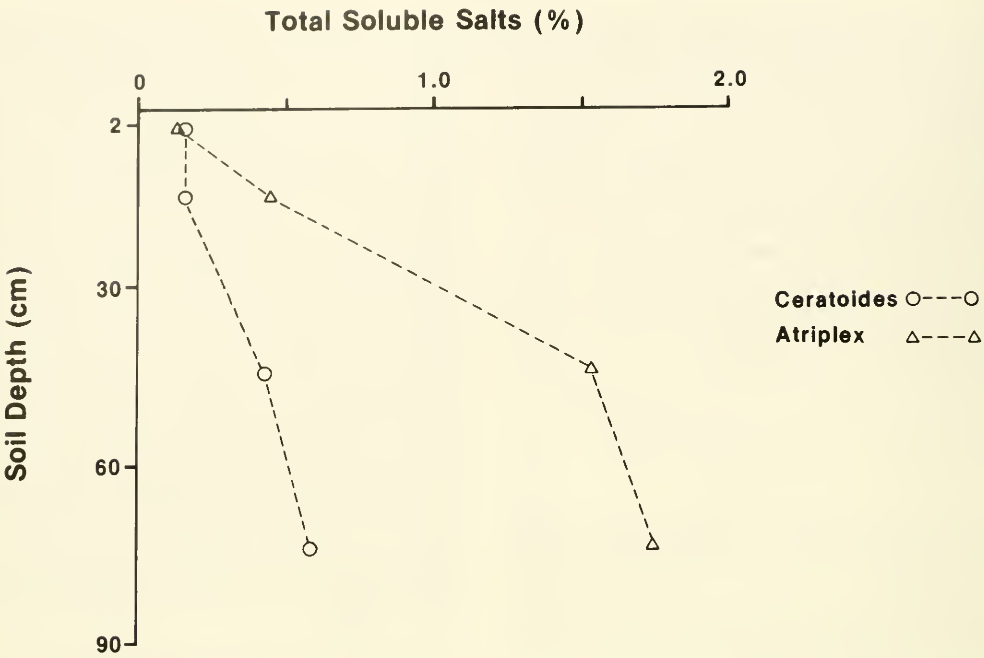

Fig. 1. The vertical distribution of total soluble salts (%) in soils under the *Atriplex* and *Ceratoides*-dominated communities, July 1968.

growth and a dieback of some aboveground tissues are usually related to the water stresses experienced during the summer (Love and West 1972).

Net Aboveground Primary Production

Estimates of average aboveground net primary production in the *Atriplex* community were significantly higher than for the *Ceratoides* community (Table 2). Only during 1968 did aboveground production of *Ceratoides* exceed the aboveground production of *Atriplex.* The differences were not statistically significant, however. Although a single end-of-growing-season harvest nearly always underestimates net aboveground primary production and the data in Table 2 should be more properly labeled "new green growth," single-harvest data prevail in the literature dealing with this type of vegetation.

Table 2. Estimates of net annual aboveground primary production (gm m^{-2} yr^{-1} ± 90% confidence intervals) in *Atriplex-confertifolia-* and *Ceratoides-lanata-*dominated communities.

	Community type	
Year	*Atriplex*	*Ceratoides*
1968	78 ± 9	83 ± 5
1969	61 ± 6	50 ± 4
1970	113 ± 12	76 ± 5
Mean	84 ± 7	70 ± 4

Similar between-communities differences in average net aboveground primary production were found in other phytomass and production studies of chenopod shrublands in Curlew Valley (Caldwell et al. 1977). In their studies, addition of litter that had fallen prior to clipping accounted for only 2% to 9% of their annual shoot production estimates. Fetcher and Trilica (1980), using six years of data gathered from the same area, reported that annual aboveground production of *Atriplex* and *Ceratoides* (also estimated from a single midsummer clipping of new growth) was well correlated with growing season (March–June) precipitation ($P \leq 0.10$ and $P \leq .009$, respectively).

The comparison of these phytomass and aboveground production data with salt desert shrub communities elsewhere (Rodin and Basilevich 1967, Holmgren and Brewster 1972, Branson et al. 1976, Osmond et al.

1980) is difficult because of differing environments, definitions, and methodologies. Herbivory and amounts of prior leaf fall are, like herein, often ignored, as are increments to stem wood on the irregularly shaped stems of these shrubs. The weight of developing fruit is included here. A greater problem, however, is determination of live and dead tissues. Desert shrubs such as *Atriplex* have a large fraction of standing dead wood. It is difficult on some *Atriplex* plants to decide what part of the plant is alive.

The reason for the small differences in means and confidence intervals for new shoot growth in Table 1 and 2 is that the former are plot based, and the latter are determined from a random selection of individual plants.

Our estimates of the weights of aboveground litter (Table 3) probably exceed the long-term averages due to drought-induced increases in mortality of plant parts following a period of above-normal precipitation prior to and early in our study period (West and Gasto 1978).

For a detailed discussion of below ground plant community dynamics at this study site see Caldwell and Fernandez (1975) and Caldwell et al. (1977). Belowground production was roughly 3.5 times that of aboveground.

Litter Turnover

Estimates of litter turnover are crucial to our considerations of mineral cycling since litter represents the largest and most readily available source of organically incorporated nutrients. Turnover of soil surface litter and the standing dead portion was estimated by dividing estimates of mean net aboveground primary production by mean aboveground litter fractions (Table 4). This was done on the assumption that, if the communities were successionally stable, or nearly so, the long-term values for new growth should equal litter fall. The true turnover coefficients are probably higher than the values in Table 4 due to likely underestimations in net primary production discussed previously.

Table 3. Estimates of aboveground litter standing crops (oven-dry gm m^{-2}) in *Atriplex*- and *Ceratoides*-dominated communities, Curlew Valley, Utah. Midsummer values for the years 1968–1970.

			Community type	
Component	Year	Type	*Atriplex*	*Ceratoides*
Shoot litter	1968	Coarse	446	–
		Fine	426	381
	1969	Coarse	479	–
		Fine	380	355
	1970	Coarse	413	–
		Fine	397	465
Average	1968–70	Coarse	446	–
		Fine	403	400

The decomposition of *Atriplex* and *Ceratoides* fine shoot litter was quite comparable, but when the coarse litter of *Atriplex* was added, a much slower recycling of minerals was suggested. The overall differences in litter turnover were closely related to growth habit (Table 4). *Atriplex* plants were larger and had a high proportion of hard, woody tissue. *Ceratoides* stems were generally less than 0.5 cm in diameter and more easily decomposed. *Atriplex* coarse litter was derived from woody stem tissue that accumulates over the life of an individual plant. More rapid decomposition of litter in the *Atriplex* community was suggested when only fine litter was considered (Table 4). Greater N content of *Atriplex* new growth compared to *Ceratoides* may be causually associated with this difference.

Root litter production could not be reliably estimated because of the difficulty in separating live and dead roots. Descriptions of the problems involved and initial attempts to deal with these important processes can be found in Caldwell and Camp (1974) and Caldwell and Fernandez (1975). Hodgkinson et al. (1978) suggests that less than 10% of the root phytomass in *Atriplex confertifolia* communities may be alive, leading to the possible conclusion that most of the belowground phytomass is litter.

Table 4. Turnover coefficients (fraction decomposed each year) and turnover time for soil surface litter (years) in *Atriplex*- and *Ceratoides*-dominated communities based on 1968–70 phytomass estimates and aboveground new growth fractions, assuming steady state conditions.

	Community type	
	Atriplex	*Ceratoides*
Turnover coefficient	0.09 (.21)[1]	0.17
Turnover time (yr)	10.1 (4.8)[1]	5.71

[1] Turnover time for easily decomposable fine litter fraction only in parentheses

Mineral Concentrations within the Compartments

Tables 5 and 6 list means and standard deviations in concentrations of selected mineral elements in various plant parts, litter, and soil in the two community types. Discussion of some major (statistically significant = within one standard deviation, to include the mean 68% of the time) descriptive differences will be followed by other reorganizations of the data, attempting to rank the elements in order of their probable roles in limiting community functions.

Concentrations of K, Na, Ca, and Mg in the new shoot growth fraction of *Atriplex* were significantly higher ($P \leq .001$, .001, .15, and .3, respectively) than in *Ceratoides*. The concentrations of elements in old shoot growth were comparable between the two species except that Na was significantly higher in *Atriplex*. The two species had similar ratios of elemental concentrations in new to old shoot growth, except for N, P, Na, Ca, and Mg. This similarity, coupled with the observation that N, K, Na and Mg concentrations were significantly higher in the new growth fraction in both species, hints at their possible limiting function (Charley 1977). In Curlew Valley, K, Na, and Mg are very abundant and soluble in soil solutions and may be taken up in quantities far in excess of metabolic need (luxury consumption).

Elemental concentrations in litter were comparable between communities except that Na was higher in the fine fraction of *Atriplex* and K was higher in *Ceratoides* litter. Statistically significantly higher Na concentrations appeared in upper-level *Atriplex* roots, and Ca was higher throughout all root depths of *Ceratoides*. Concentrations of elements in the soils showed pronounced, similar decreases of C, N, and K with increasing depth in both community types. *Atriplex* soils had significantly greater P and Na at all depths.

Interpretations of nutrient concentrations at one point in time and space are limited in value because of translocation and the known seasonal dynamics of the elements (Breckle 1976). Nevertheless, some relationships with anatomical and physiological knowledge can be discussed.

Direct comparison of these data with those of prior studies (Wiebe and Walter 1972, Moore et al. 1972, Breckle 1974, 1976) at the same site is difficult since the earlier studies dealt with soluble forms (including some anions) in expressed sap from fresh growth of leaves and stems rather than the ash form concentrations presented here. The same general species differences, however, were found in the new growth fractions.

Atriplex is known to accumulate salts in vesicular epidermal cell leaf hairs that eventually rupture and deposit salts on the leaf

TABLE 5. Means and standard deviations of elemental concentrations (mg g^{-1}) in various components of a *Ceratoides-lanata*-dominated ecosystem, Curlew Valley, Utah. Average of 1968, 1969, and 1970 samples.

	C	N	P	K	Na	Ca	Mg
SHOOTS							
New growth		11.9 ± 2.4	1.1 ± .1	13.5 ± 1.0	.9 ± .1	19.5 ± 2.5	3.95 ± .47
Old growth		10.9 ± 1.2	1.1 ± .1	6.6 ± .8	.8 ± .1	22.2 ± 2.2	3.53 ± .61
LITTER							
		13.7 ± 1.4	1.2 ± .2	4.0 ± 0.4	.5 ± 1.7	15.7 ± 1.7	2.97 ± .43
ROOTS							
0–30		16.3 ± 1.5	1.4 ± .1	5.1 ± .9	2.0 ± 1.2	47.5 ± 5.5	5.14 ± .94
30–60		16.1 ± 1.8	1.5 ± .1	5.1 ± .7	3.4 ± 1.5	52.9 ± 3.9	6.68 ± .47
60–90		18.1 ± 2.6	1.6 ± .1	5.1 ± .6	3.5 ± 1.3	53.1 ± 3.3	6.91 ± .51
SOIL							
0–2	14.8 ± 1.6	1.2 ± .3	.8 ± .1	2.5 ± .5	.3 ± .2	5.8 ± .9	.33 ± .02
2–30	7.9 ± 1.7	.7 ± .1	.6 ± .1	2.0 ± .4	.5 ± .3	5.4 ± 1.3	.31 ± .05
30–60	6.5 ± 1.0	.6 ± .1	.6 ± .1	1.9 ± .3	1.8 ± .5	4.9 ± 1.0	.37 ± .07
60–90	5.3 ± 1.0	.4 ± .1	.6 ± .1	1.6 ± .4	3.3 ± .8	4.8 ± 1.4	.45 ± .11

surface (Osmond et al. 1980). *Atriplex confertifolia* sampled elsewhere had high concentrations of Na and other alkaline elements (Wallace and Romney 1972, Wallace et al. 1973a, 1973b, 1974, 1975). *Ceratoides* is thought to exclude Na and some other cations at the root-soil interface (Breckle 1976). It accumulates Ca, however, particularly in the roots. Classification of *Atriplex* as a euhalophyte and *Ceratoides* as a calciohalophyte (Walter 1979) is supported by these data.

It is interesting that the two species differed in Ca distribution patterns between new and old aboveground growth and root phytomass. Ca metabolism has been linked with the salinity tolerance of certain crop species (Epstein and La Haye 1969). The Ca:Na ratios differ in the two species studied here and, at least in Curlew Valley, *Atriplex* takes root in a saltier soil than does *Ceratoides* (Fig. 1). Seasonal variation in Ca:Na ratios of plant tissue of the species are known (Breckle 1976); nevertheless, Ca:Na interactions are worthy of further investigation. Breckle (1974, 1976) ascribed a possible functional role to the high Na content of *Atriplex confertifolia,* hypothesizing that it allows this species to take up soil moisture and carry on photosynthesis for a longer period through the summer than can *Ceratoides*. The lower anionic concentrations he found may have been related to the bonding of cations by high amounts of organic acids (chiefly oxalic) in these chenopods (Wiebe and Walter 1972). How much this mechanism differs between the two species is unknown.

Mineral Content of the Ecosystems

Comparisons of mineral contents at the ecosystem level require multiplication of compartmental elemental concentrations by phytomass and soil bulk density to derive standing crops of minerals (mineralomasses, Duvigneaud and DeSmet 1975). Although this approach overlooks the seasonal variation in both mineral concentrations and phytomass, it allows a graphical comparison (Fig. 2) of the pools of the various minerals to be expected during midsummer. For most elements, the beginning of the growth period in spring is the time of highest mineral concentrations (Caldwell et al. 1971, West 1972, Breckle 1976) in new growth fractions. There is not as much seasonal variation in either the old growth aboveground phytomass or the mineral content of surface litter, belowground phytomass, and soil compartments (Caldwell et al. 1971, West 1972,

Table 6. Means and standard deviations of elemental concentrations (mg g^{-1}) in various components of an *Atriplex-confertifolia*-dominated ecosystem, Curlew Valley, Utah. Average of 1968, 1969, and 1970 samples. P = probability level at which a given value for *Atriplex* is different from that of *Ceratoides*.

	C	N	P	K	Na	Ca	Mg
SHOOTS							
New growth		13.9 ± 2.6	1.0 ± .2	21.5 ± 1.1°°	8.1 ± .2°°	31.3 ± 5.0‡	5.92 + 1.44†
Old growth		9.8 ± .8	1.0 ± .1	9.5 ± 3.1	5.7 ± .7°°	18.2 ± 5.4	3.56 ± 1.00
LITTER							
Fine		12.6 ± 1.3	1.5 ± .2	3.0 ± .3	1.8 ± .2	15.7 ± .7	2.57 ± .21
Coarse		10.0 ± 1.0	.9 ± .1	3.2 ± .5	1.9 ± .4	14.5 ± 3.2	2.07 ± .67
ROOTS							
0–30		16.7 ± 1.3	1.5 ± .2	6.3 ± 1.3	4.4 ± 1.0†	32.8 ± 7.7†	5.96 ± 2.20
30–60		17.2 ± 2.0	1.6 ± .2	6.7 ± 1.2	5.1 ± 1.3	35.6 ± 8.2‡	6.14 ± 2.20
60–90		18.8 ± 2.3	1.8 ± .1	7.0 ± 1.1	5.7 ± 1.3	38.2 ± 9.0†	6.35 ± 2.22
SOILS							
0–2	17.6 ± 1.2	1.6 ± .6	1.1 ± .1	2.6 ± .5	.9 ± .2‡	5.7 ± 1.5	.33 ± .05
2–30	8.4 ± 1.0	.8 ± .1	.9 ± .2	2.7 ± .6	2.7 ± .9‡	5.3 ± 1.1	.27 ± .06
30–60	7.5 ± .7	.6 ± .1	.8 ± .1	1.8 ± .4	5.8 ± 1.4°	5.3 ± .7	.39 ± .09
60–90	6.7 ± .7	.5 ± .0	.7 ± .1	1.2 ± .4	7.2 ± 1.2°	5.4 ± .9	.60 ± .05

†P ≤ .3
‡P ≤ .15
°P ≤ .05
°°P ≤ .001 Probability level at which the given value for *Atriplex* ecosystems differs from the parallel value for the *Ceratoides* ecosystem (Table 5)

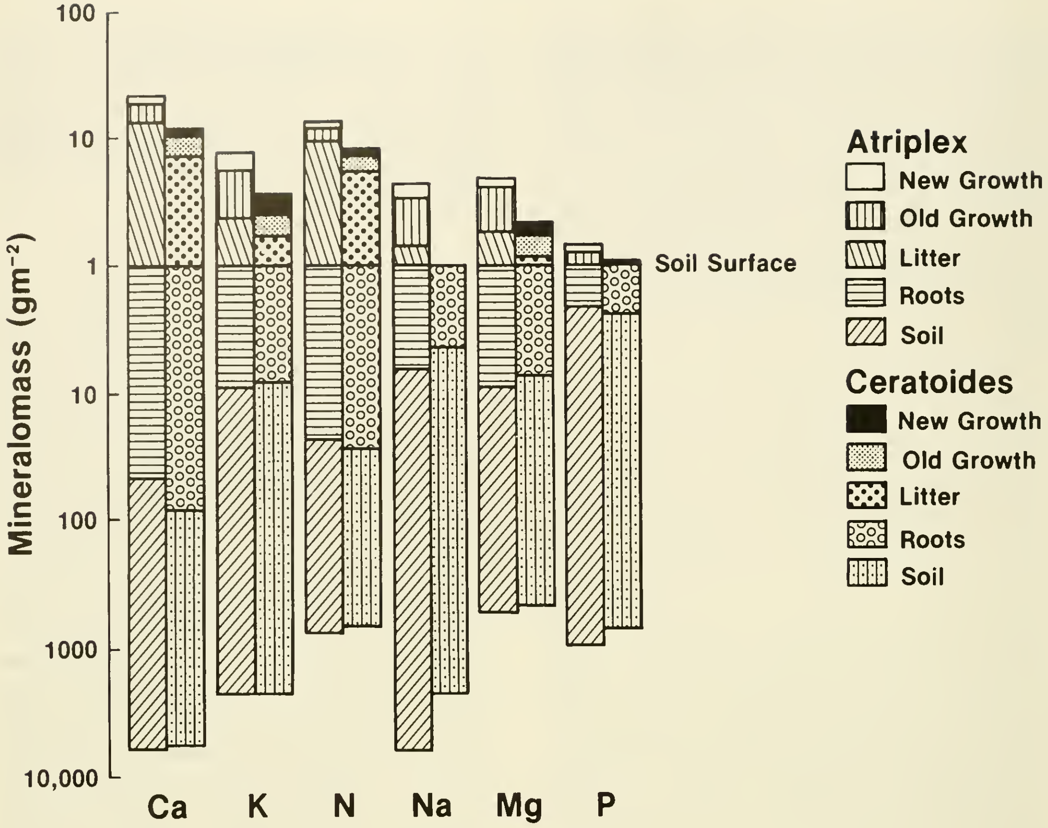

Fig. 2. Graphical comparison of mineralomass of various mineral elements in *Atriplex*- and *Ceratoides*-dominated ecosystems. Average of element concentration times average phytomass values for 1968, 1969, and 1970. Soil profile considered to a depth of 90 cm July 1968 only.

Breckle 1976). Nitrogen is an exception to the above generalization, which has been extensively discussed elsewhere (West and Skujins 1977, 1978).

Nearly equivalent pools of mineral elements were found in the two ecosystems. Carbon has been discussed elsewhere (Caldwell et al. 1977). Ca was the greatest contributor to the mineralomass of both ecosystems. The *Atriplex*-dominated ecosystem had slightly higher accumulations of Ca, but *Ceratoides* had more in new aboveground growth and plant tissue in general. There is less K accumulated aboveground, particularly in the new growth portion of the *Ceratoides* system. More nitrogen was accumulated in the *Atriplex* system. The soils of the *Atriplex* system also had more Na and distinctly more was incorporated into phytomass, making the differences the greatest of any of the elements studied. The *Atriplex* ecosystem had the most plant-incorporated Mg and P, with the highest proportions in aboveground compartments. This is directly related to the small differential concentrations in aboveground and belowground fractions and the somewhat higher aboveground production of *Atriplex.*

Concentrations or pools tell us nothing definitive about nutrient availability. In fact, we know that much of the soil organic matter reserve is "bound" and may be entirely of microbial origin (Kang and Felbeck 1965). Nutrient turnover time for the aboveground portion of the system could be approximated by dividing litter by new growth phytomass (Table 4). To estimate nutrient turnover in the entire community, belowground production has to be estimated and heroic assumptions about community stability made. Although such calculations would have suggested which elements might be in critical supply, we did not calculate them because of problems discussed above.

Another way of inferring which elements could be limiting is to look at the presence or absence of biological magnifications during the decomposition of fine litter compared to new growth (Charley 1977). Such an analysis can be used as a basis for separating the major minerals analyzed into two groups. N and P show increased concentrations in partially decomposed litter compared to new growth, whereas K and Na concentrations are less in litter compared to new growth. N and P remain in short supply in soil until they become excess metabolites in the absence of suitable high carbon substrates. K and Na are easily leached and are generally not needed in large quantities for decomposition processes. They also appear in excessive quantities as soluble soil salts.

Table 7 shows amounts of nitrogen and phosphorus taken up in annual shoot production in *Atriplex* and *Ceratoides* communities. These amounts are very small in comparison to total inventories. They are significant, however, when compared to amounts in easily decomposable high carbon substrates such as fine litter. When N in new growth was compared to N in litter, average turnover times of 4.6 and 6.8 years were computed for *Atriplex* and *Ceratoides*, respectively. These values compare closely to those computed on a phytomass basis (Table 4). Close monitoring of inorganic soil nitrogen supported this concept, showing gradual buildup of NH_4^+ and NO_3^- in the surface soil (Bjeeregaard 1971). This is later carried into the rooting zone by significant rainfall (Osmond et al. 1980).

Carbon:nitrogen ratios can be used to determine the extent of decomposition of carbon-based substrates as mineralization occurs (West and Skujins 1977, 1978). *Ceratoides* and *Atriplex* fine litter exhibit C:N ratios of 38.4 and 41.4, respectively. The *Atriplex* coarse litter C:N ratio is 46.5. C:N ratios in soil varied from 10.5 at the surface to 13.3 at 60–90 cm for *Atriplex*, and from 10.7 to 15.7 for *Ceratoides*. "Terminal" or steady state soil C:N ratios appear to be related to increasing soluble salt concentrations (Fig. 1), and maximum ratios occur at 60–90 cm depths.

Table 7. Estimates of nitrogen and phosphorus uptake in aboveground production of *Atriplex*- and *Ceratoides*-dominated communities. Averages of 1968–70 production estimates were used.

	Community type			
	Atriplex		*Ceratoides*	
Nutrient	mg g^{-1}D.W.	g m^{-2}	mg g^{-1}D.W.	g m^{-2}
Nitrogen	14	1.2	12	0.8
Phosphorus	1.0	0.9	1.1	0.1

Although these data and inferences are intrinsically interesting and valuable for related considerations such as animal nutrition, much remains to be done to discover what soil-held nutrients are limiting to plant growth in deserts once the primary constraint of available soil moisture is exceeded (West 1983). Further inferences as to which elements may act as secondary limiting factors can only be definitively stated after direct experimentation.

Since the *Atriplex*-dominated community is more productive than the *Ceratoides*-dominated community and has somewhat greater plant litter and microphytic crusts that stabilize the soil and fix more nitrogen (Bjerregaard 1971), we should not be concerned that the probable replacement of *Ceratoides* by *Atriplex confertifolia* on the sites studied (Dzurec 1981) will necessarily result in greater erosion. Although primary productivity is higher with *Atriplex*, its spines protect it from heavy livestock utilization. This appears to be a feedback mechanism protecting the land as well as the plants from individual damage.

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LITERATURE CITED

Bjerregaard, R. S. 1971. The nitrogen budget of two salt desert shrub plant communities of western Utah. Unpublished dissertation, Utah State Univ., Logan. 100 pp.

Branson, F. A., R. F. Miller, and J. S. McQueen. 1976. Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. Ecology 57:1104–1124.

Breckle, S.-W. 1974. Wasser-und Salzhaltnisse bei Halophyten der Salzsteppe in Utah, USA. Ber. Deutsch. Bot. Ges. 87:589–600.

——. 1976. Zur Okologie und zer den Mineral-stoffverhaltnissen absalsalzender and nichtabsalender Xerohalophyten Unter besonderer Berucksichtigung von Untersuchungen an *Atriplex confertifolia* und *Ceratoides lanata* in Utah/U.S.A. Dissertationes Botanicae Band 35, J. Cramer, Vadez, Habilitationsschrift Mathematisch–Naturwissenschartliche, Facultat der Universitat Bonn. 169 pp.

Brewster, S. R., Jr. 1968. A study of effectiveness of precipitation in the salt desert shrub type. Unpublished thesis, Brigham Young Univ., Provo, Utah. 67 pp.

Caldwell, M. M. 1975. Primary production of grazing lands. Pages 41–73 *in* J. P. Cooper, ed., Photosynthesis and productivity in different environments. Cambridge Univ. Press, IBP Vol. 3.

Caldwell, M. M., and L. B. Camp. 1974. Belowground productivity of two cool desert communities. Oecologia (Berl.) 17:123–130.

Caldwell, M. M., and O. A. Fernandez. 1975. Dynamics of Great Basin shrub root systems. Pages 38–51 *in* Hadley, N. F. ed., Dowden, Hutchinson, and Ross, Physiological Adaptations of desert organisms. Stroudsburg, Pennsylvania.

Caldwell, M. M., N. E. West, and P. J. Goodman. 1971. Autecological studies of *Atriplex confertifolia and Eurotia lanata.* US/IBP Desert Biome Res. Memo 71-4. Utah State Univ., Logan. 16 pp.

Caldwell, M. M., R. S. White, R. T. Moore, and L. B. Camp. 1977. Carbon balance, productivity, and water use by cold winter desert shrub communities dominated by C_3 and C_4 species. Oecologia (Berlin) 29:275–300.

Chapman, H. D., and P. F. Pratt. 1961. Methods of analysis of soils, plants, and waters. Univ. of California, Davis, Div. Agric. Ser. 309 pp.

Charley, J. L. 1977. Mineral cycling in rangeland ecosystems. Pages 215–256 *in* R. Sosebee, ed., Rangeland plant physiology. Soc. Range Manage., Range Sci. Series 4, Denver, Colorado.

Duvigneaud, P., and S. Denaeyer-DeSmet. 1975. Mineral cycling in terrestrial ecosystems. Pages 133–154 *in* D. E. Reichle, J. F. Franklin, and D. W. Goodall, eds., Productivity of world ecosystems. U.S. National Academy of Sciences, Washington, D.C.

Dzurec, R. S. 1980. Carbon isotope ratios of soil organic matter and their use in assessing community composition changes in Curlew Valley, Utah. Unpublished thesis, Utah State Univ., Logan. 59 pp.

Eardley, A. J., V. Gvosdetsky, and R. E. Marsell. 1957. Hydrology of Lake Bonneville and sediments and soils of its basin. Bull. Geol. Soc. Amer. 68:1141–1202.

Epstein, E., and P. A. LaHaye. 1969. Salt toleration by plants: enhancement with calcium. Science 166:395–396.

Fetcher, N., and M. J. Trilica. 1980. Influence of climate on annual production of seven cold desert forage species. J. Range Manage. 33:35–37.

Gasto, J. M.1969. Comparative autecological studies of *Eurotia lanata* and *Atriplex confertifolia.* Unpublished dissertation, Utah State Univ., Logan. 278 pp.

Gates, D. H., L. A. Stoddart, and C. W. Cook. 1956. Soil as a factor influencing plant distribution of salt deserts of Utah. Ecol. Monogr. 16:155–175.

Hodgkinson, K. C., P. S. Johnson, and B. E. Norton. 1978. Influence of summer rainfall on root and shoot growth of a cold-winter desert shrub, *Atriplex confertifolia* Oecologia (Berlin) 34:353–362.

Holmgren, R. C., and S. F. Brewster, Jr. 1972. Distribution of organic matter reserve in a desert shrub community. USDA Forest Service Res. Pap. INT-30. 15 pp.

Jackson, M. L. 1958. Soil chemical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 498 pp.

Kang, K. S., and G. T. Felbeck, Jr. 1965. A comparison of alkaline extract of tissues of *Aspergellus niger* with humic acids from three soils. Soil Sci. 99:175–181.

Love, L. D., and N. E. West. 1972. Plant moisture stress patterns in *Eurotia lanata* and *Atriplex confertifolia.* Northwest Sci. 46:44–51.

Mitchell, J. E., N. E. West, and R. W. Miller. 1966. Soil physical properties in relation to plant community patterns in the shadscale zone of northwestern Utah. Ecology 47:627–630.

Moore, R. T., S.-W. Breckle, and M. M. Caldwell. 1972. Mineral ion composition and osmotic relations of *Atriplex confertifolia* and *Eurotia lanata.* Oecologia (Berlin) 11:67–78.

Osmond, C. B., O. Bjorkman, and D. J. Anderson. 1980. Physiological processes in plant ecology: toward a synthesis with *Atriplex.* Springer-Verlag, New York. 480 pp.

Rodin, L. E., and N. I. Basilevich. 1967. Production and mineral cycling in terrestrial vegetation. (English translation edited by G. E. Fogg.). Oliver and Boyd, London. 288 pp.

U.S. Salinity Laboratory. 1954. Diagnosis and improvement of saline and alkali soils. Agricultural Handbook No. 60. Government Printing Office, Washington, D.C. 160 pp.

Wagner, F. H. 1980. Integrating and control mechanisms in arid and semiarid ecosystems—consideration for impact assessment. Pages 145–158 *in* Proc. Symposium on Biological Evaluation of Environmental Impact. Council on Environmental Quality and Fish and Wildlife Service, U.S. Dept. Interior, Washington, D.C.

Wallace, A., R. T. Mueller, and E. M. Romney. 1973. Sodium relations in desert plants. II. Distribution of cations in plant parts of three species of *Atriplex.* Soil Sci. 115:390–396.

Wallace, A., and E. M. Romney. 1977. Radioecology and ecophysiology of desert plants at the Nevada test site. U.S. Atomic Energy Commission, Office of Information Services, Oak Ridge, Tennessee. TID-25954. 474 pp.

Wallace, A., E. M. Romney, and V. O. Hale. 1973. Sodium relations in desert plants: location contents of some plant species from Mojave and Great Basin deserts. Soil Sci. 115:284–291.

Wallace, A., E. M. Romney, J. W. Cha, and G. V. Alexander. 1974. Sodium relations in desert plants. III. Cation-anion relationships. Three species which accumulate high levels of cations in leaves—*Lycium andersonii, Atriplex confertifolia, Atriplex hymenelytra.* Soil Sci. 118:397–401.

Walter, H. 1979. Vegetation of the earth and ecological systems of the geo-biosphere. 2d ed. Springer-Verlag, New York. 274 pp.

West, N. E. 1972. Biomass and nutrient dynamics of some major cold desert shrubs. US/IBP Desert Biome Res. Memo. 72-15. Utah State Univ., Logan. 24 pp.

____. 1981. Nutrient cycling in desert ecosystems. Pages 301–324 *in* D. W. Goodall and R. A. Perry, eds., Aridland ecosystems: structure, functioning and management. Vol. 2, IBP Vol. 17. Cambridge Univ. Press, Cambridge.

____. 1983. Intermountain salt-desert shrublands. Pages 375–398 *in* N. E. West, ed., Temperate deserts and semi-deserts. Ecosystems of the World, Vol. 5. Elsevier Sci. Publ. Co., Amsterdam.

West, N. E., and M. M. Baasher. 1968. Determination of adequate plot size by use of mean distance between salt desert shrubs. Southwestern Nat. 13:61–74.

West, N. E., and J. Gasto. 1978. Phenology of aerial portions of shadscale and winterfat in Curlew Valley, Utah. J. Range Manage. 31:43–45.

West, N. E., and J. Skujins. 1977. The nitrogen cycle in North American cold-winter semi-desert ecosystems. Oecol. Plant. (Paris) 12:45–53.

____, eds. 1978. Nitrogen in desert ecosystems. US/IBP Vol. 9. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania. 309 pp.

Whittaker, R. H. 1961. Estimation of net primary production of forest and shrub communities. Ecology 42:177–180.

Wiebe, H. H., and H. Walter. 1972. Mineral ion composition of halophytic species from northern Utah. Amer. Midl. Nat. 87:241–245.

BIONOMICS OF THE CONE SPITTLEBUG, *APHROPHORA CANADENSIS* (HOMOPTERA: CERCOPIDAE) ON MUGO PINE IN IDAHO

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Abstract.— The spittlebug, *Aphrophora canadensis* Walley (Homoptera: Cercopidae), was discovered at Moscow, Idaho, in 1979 infesting *Pinus mugo* Turra, an exotic ornamental pine. Masses of spittle, densely populated with nymphs, have continued to be abundant since then. The nymphs congregated and fed mainly on cones and did not cause visible reddening of foliage that is typical of other pine-infesting spittlebugs. Immature stages and behavior are described for the first time and are compared to other nearctic pine-infesting species. Beginning in mid-August, eggs were laid under fascicle sheaths at the bases of needles, where they overwintered. Nymphs appeared in late April and began transforming to adults in mid-July. Mating occurred from early August to late September. Adults lingered in diminishing numbers until mid-October.

In 1979, profuse masses of white spittle (Fig. 1A) of *Aphrophora canadensis* Walley appeared on 20-year-old mugo pine (*Pinus mugo* Turra) at Moscow, Idaho. We were curious about the sudden abundance of the spittle and the propensity of nymphs to congregate and feed on cones (Fig. 1B) although no cercopid is listed among North American cone and seed insects by Hedlin et al. (1980). The host is a European pine (Critchfield and Little 1966) widely grown as an ornamental in temperate North America.

A. canadensis was originally described from Victoria B.C. by Walley (1928). Doering (1941) further described the adult stage while revising the genus. Kelson (1964) observed a closely related, undescribed species[3] on Monterey pine (*Pinus radiata* D. Don) and knobcone pine (*Pinus attenuata* Lemmon) in California.

Other pine-infesting *Aphrophora* species in North America include the Saratoga spittlebug, *A. saratogensis* (Fitch) (Ewan 1961, Wilson 1978); the pine spittlebug, *A. cribrata* (Walker) (=*parallela* Say of Speers 1941) (Hamilton 1982); and *A. permutata* Uhler (Kelson 1964). The former two species are eastern; *permutata* occurs in the west. The adults of *saratogensis* and *permutata* feed on coniferous hosts, laying their eggs under bud and bark scales; the nymphs develop on understory herbaceous vegetation. All life stages of *cribrata* and *canadensis* feed exclusively on coniferous hosts.

The host plants and oviposition site of *canadensis* are reported here for the first time. Other new information involves locality records, description of immature stages, seasonal history, and behavior.

METHODS

The study area was primarily on the grounds of the Forestry Sciences Laboratory, Moscow, Idaho, at 790 m elevation. Spittlebugs were observed annually from 1979 through 1982 on mugo pine outside our insectary. Other colonies were observed and collected on 18-year-old lodgepole pine (*P. contorta* Dougl.) and ponderosa pine (*P. ponderosa* Lawson) at a residence 6 km from the laboratory. *Aphrophora canadensis* spittle masses and nymphs were observed fortuitously on older lodgepole pine at McCall, Idaho (ca 1600 m elevation), and younger lodgepole pine 27 km north of Sandpoint, Idaho (ca 750 m elevation). We also noted an infestation on mugo pine in Pullman, Washington, 16 km west of our primary study site.

During 1981, the location of eggs, nymphs, and adults on host trees, and their behavior,

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[3] Reported by Kelson to be *A. canadensis*, but determined to be new by Dr. K. G. A. Hamilton, pers. comm., 1 March 1982.

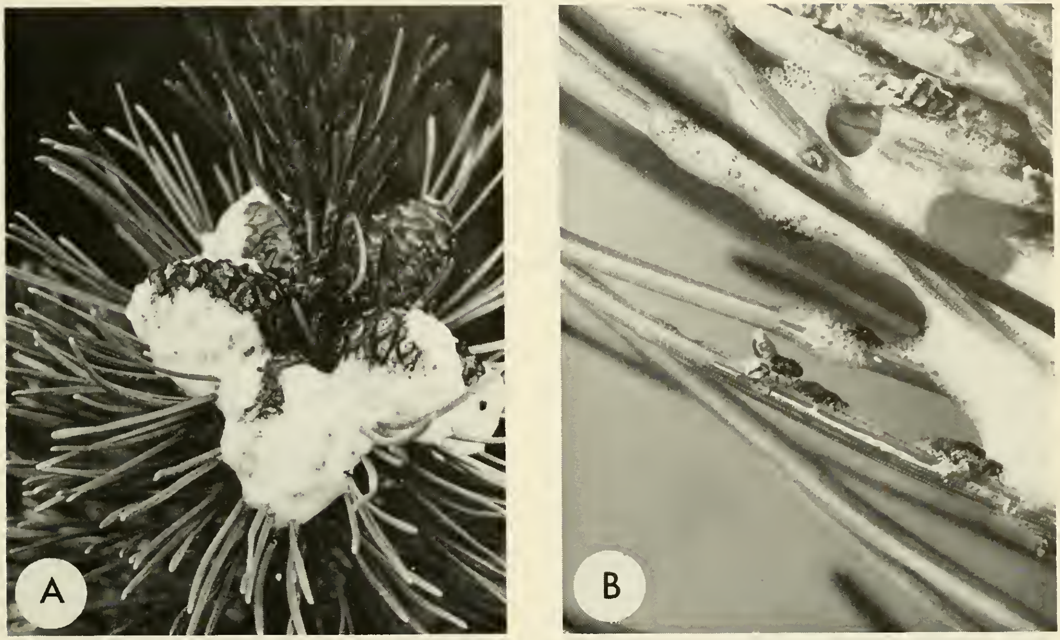

Fig. 1. Nymphs commonly formed spittle masses on cones (A), but young nymphs sometimes infested needles (B), particularly on branches that lacked cones.

were observed intensively outdoors under natural conditions. Eggs were collected and incubated in the laboratory on 18 February. Other eggs were observed on host trees weekly until hatching began 30 April; thereafter, approximately 100 nymphs were collected weekly until adults appeared 14 July. Nymphs were preserved in 70% alcohol. The five nymphal stadia were described and their proportional abundance tabulated by collection date. Approximately 50 adults of each sex were preserved for study and identification. Because the genitalia tended to distort upon drying, about one-half of the collected adults were stored in alcohol until examined.

DAMAGE

Four generations of *canadensis* had little effect on the appearance of their mugo pine hosts except for the masses of white spittle that were present from May to mid-July. Foliage was retained normally. Absent was the severe reddening of foliage as reported for other conifers in the literature previously cited on *saratogensis* and *cribrata*.

Injury by some spittlebugs has been associated with fungus infection. On red pine (*Pinus resinosa* Ait.), *saratogensis* damage has led to infection by burn blight fungus (*Nectria cucurbitula* Tode ex Fr.) (Hepting 1971). Damage to Scotch pine (*Pinus sylvestris* L.) by *cribrata* has been worsened by infection with pine twig blight (*Diplodia pinea* (Desm.) Kickx.) (= *Sphaeropsis ellisii* Sacc.) (Speers 1941). Our microscopic examination of mugo pine needles disclosed circular yellowish or brownish areas on the basal portion of needles where nymphs had fed, but the injured areas were well defined and did not enlarge, coalesce, or kill needles. The propensity for *canadensis* nymphs to infest cones undoubtedly limited the amount of needle damage.

LIFE STAGES

Egg

The egg (Fig. 2) is pearl white initially, becoming turquoise with maturity. It is elongated teardrop shaped, average length 1.74 mm, and width 0.56 mm, and is more acutely tapered at the emergence end, which has a black, scablike subapical plate approximately one-fifth the egg's length. No mention was made of this plate for the pine spittlebug (Speers 1941) or the Saratoga spittlebug

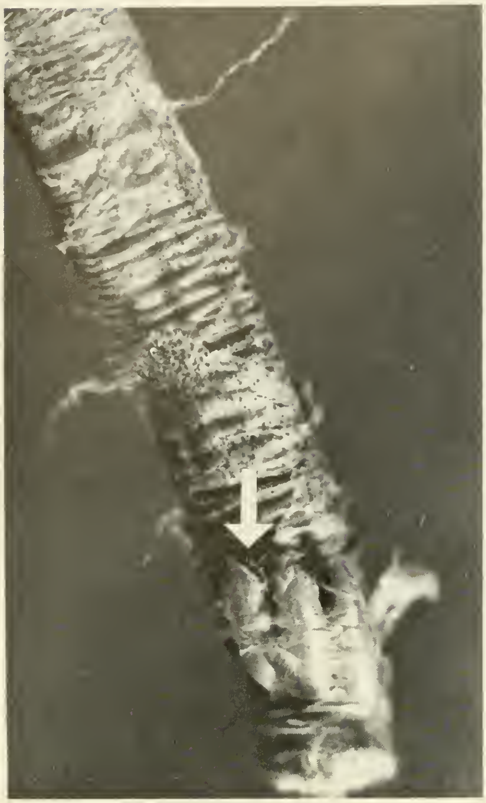

Fig. 2. Eggs were deposited under needle fascicle sheaths. Scablike apical plate is visible on egg at left (arrow).

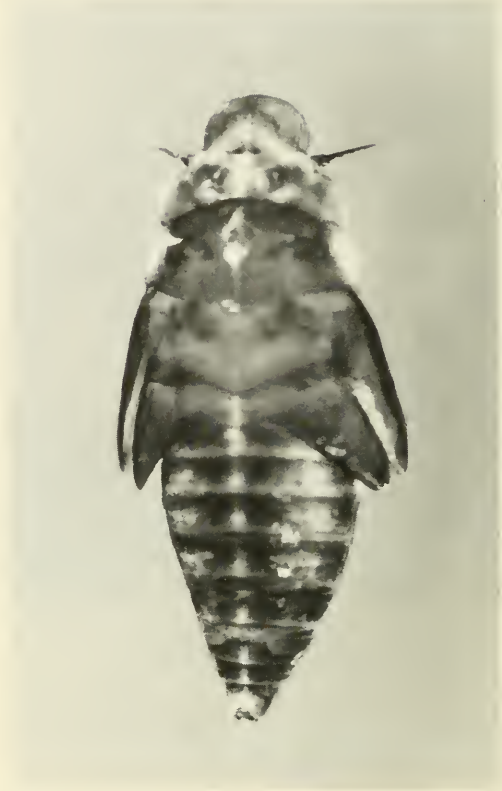

Fig. 3. Instar 5 nymph.

(Ewan 1961). The plate is narrow and lanceolate. The smooth chorion is rubbery and durable. It overlays an inner, darker covering, from which it can be easily separated by rupturing the chorion with pointed forceps. The inner covering of the egg is finely pebbled in appearance. An orangish yolk is visible in overwintered eggs.

Nymph

There are five nymphal instars, the first four of which appear to the unaided eye nearly identical except for size. Instar 5 (Fig. 3) exhibits a light and dark color phase, the lighter of which is more common and similar to the previous instars. The body length ranges from about 1.7 mm for the 1st instar to 6 to 8 mm for the 5th. The head widths for each instar are shown in Table 1.

Kelson (1964) described the head and thorax of instars I to IV of his undescribed species as "shiny black." In the first four instars of our specimens, the shieldlike head, thoracic nota, and appendages are uniformly medium to dark brown with amber or ivory-colored articulations and with a thin median amber line running dorsally over the frons and down the thorax. The sternum is lighter in color, more golden brown and ivory. The eyes are red. The frons, inflated like a riot-officer's helmet, appears especially dark and shining in the first two instars. In the later instars, the golden horizontal striations on the frons appear increasingly gridlike. The squared-off lateral edge of the dark pronotum is a contrasting ivory color in all but the first instar.

The abdomen shows the greatest developmental variation, differences in which will be described by instar hereafter. The abdomen of the first four instars is tangerine-yellow except for the caudal segments discussed hereafter, and has a localized bright raspberry red blush along the sides of the widest segments. The median line of the thorax continues as a yellow-stained furrow to abdominal segment 9. The laterotergal margin of segments 3 to 9 is folded under along the cream-colored sternum and equipped, especially in the older instars, with opposing, sometimes overlapping plates that open and shut against one another ventrally to form spit-bubbles. The venter of the third segment, like that of the pine spittlebug (Speers 1941), bears a prominent nipplelike process which, we believe, acts as a gasket or air-seal when the tergal plates draw shut. The plates of this segment truncate basally to fit against the correspondingly modified fleshy shelf on each side of the nipple. Protruding beyond segment 9 is a small, truncate anal segment ringed apically by two pairs of brown ridges and possessing a brown ventral plate. This segment is similar in all instars.

Instar I.— The head and pronotum are entirely dark brown. Abdominal tergites 3 to 6 are stained raspberry red laterally; segments 7 to 8 are orangish yellow dorsally. The tube-shaped segment 9 is divided lateroventrally into two sclerotized dark brown tergal lobes resembling bomb-bay doors. The tergal lobes of segments 3 to 8 are unpigmented, with thin crescent-shaped borders. The shallow, concave sternite 9 bears a brown, flat trapezoidal plate, from which the genitalic structures will arise.

Instar II.— Golden brown gridlike striations are faintly visible on the frons. Pronotum in this and the following instars have cream-colored lateral edges. Raspberry blush is present on abdominal segments 3 to 6. The pink blush mentioned by Kelson (1964) is reduced to segments 4 to 6. Segments 7 and 8 are ivory colored except where stained yellow by the dorso-median furrow. A smoky brown patch on the side of segment 8 is faintly evident. The dark tergal sclerites of segment 9 meet dorsally in this instar to form an irregular saw-toothed ring with an ivory edge. In addition, the laterotergal lobes of segments 8 and 7 (and sometimes 6) are variably tanned smoky brown, especially near the anterior corner of each lobe. The inner surface of the caudal lobes is likewise sclerotized, doubly reinforcing the "doors" of the bubble-chamber.

Table 1. Head widths of the instars of *A. canadensis*.

Instar	No.	Head width (mm)	
		Average	Range
I	20	0.64	0.57–0.68
II	20	0.86	0.81–0.91
III	20	1.22	1.15–1.28
IV	20	1.72	1.55–1.80
V (♀)	17	2.39	2.30–2.60
(♂)	18	2.21	2.05–2.40

The pregenital plate of segment 9 is shallowly cloven medially, and sometimes a light brown, heart-shaped process may be evident at its base.

Instar III.— Head is medium brown with golden brown joints and striations. Wing pads are faintly evident, but not at all expanded posteriorly. Raspberry suffusion is reduced to abdominal segments 4 to 6; tergites 7 and 8 are ivory, with smoky patches developing laterally and ventrally, especially on 8. Tergite 9 is darkly sclerotized and subcylindrical in shape. Pleural lobes of segments 3 to 9 are edged with light brown; scooplike borders are still crescent shaped, though wider than in previous instars.

Two similar pairs of genitalic buds have emerged from the pregenital structures between segments 8 and 9. We still could not differentiate between sexes at this stage.

Instar IV.— Golden-brown frons is decidedly lighter than the dark brown vertex and thoracic tergites. Without magnification, the latter appear blackish, especially in living specimens. Rudimentary wing pads are present, appearing as dark notal extensions with cream undersides.

Abdominal coloration is as in the previous instar. Segment 9 is completely sclerotized dorsally and laterally, with in-rolled edges shutting together ventrally. Segments 7 and 8 are now darkly patched along the sides just above the pleural margin and to the rear of the raspberry blush on the middle segments. The borders of all abdominal pleural lobes are stained smoky brown and have grown into large, flexible, incisorlike plates resembling fish scales.

Though still rudimentary, the genitalia of either sex can be differentiated in this instar. In the female, the two pairs of genitalic buds have become lobelike and dissimilar. The outermost pair, which arise on segment 8, are parallel and contiguous along their midline, resembling harem trousers; the lobes of the inner pair are broadly separated and lie off to the sides. In the male, the two pairs of phallic lobes are alike, each pair being cleft, and they lie stacked like boxer shorts, one atop the other.

Instar V.— About one-fifth of the individuals are melanistic. The females are larger than the males, and the dark phase of each is slightly larger in size than the light phase:

Color phase	Female Av. (Range)	Male Av. (Range)
	mm	mm
Light	2.37 (2.3–2.5)	2.20 (2.1–2.3)
Dark	2.42 (2.3–2.6)	2.23 (2.05–2.4)

Ewan (1961) mentioned that instar 5 Saratoga spittlebugs darkened from tan to light brown later in the stadium. Ours remained either distinctly light or dark. Speers (1941) observed melanism only in male pine spittlebugs, but both sexes of our specimens displayed both color phases. Kelson (1964) did not mention any melanism or color dimorphism in specimens of the related, undescribed species.

The most striking color difference between these variants occurs in the abdomen, as described later. In both color phases, the head and thorax are a lighter brown than in the previous instars, especially the clypeus, which is now golden straw colored, with light brown striations. The vertex is the color of the striations and has acquired two ocelli, outlined in bright strawberry pink, like the eyes. A pair of amber patches lie between the posterior margin of the compound eyes and the ocelli.

The pronotum is uniformly medium brown and sometimes darker than the other two thoracic nota. The lateral borders vary from cream to yellow. The meso- and metanota are likewise a uniform brown, marked only with a thin median line. In contrast, Kelson (1964) described "2 white spots" on the metathorax of his undescribed species, "centered between the midline and the lateral edges." The dark wing pads coattail down nearly as far as the third abdominal segment. The upper pair is margined ivory along the anterior rim and has, on each bud, two vague ivory submarginal blotches. The underside of the nymph, including the wing pads, is predominantly golden-ivory, highlighted in brown.

The instar 5 abdomen is more tanned than that of the previous instars. As a result, the bright colors are less pronounced, as though seen through thick isinglass. In light phase specimens, the tergites are tan, with a faded salmon blush along the sides of segments 4 to 6. The margins of tergites 7 to 8 have patches as dark as the thorax, but the cylindrical segment 9, in contrast with that of the previous instars, is nearly as light as the rest of the abdomen. A faint yellow-stained broken median line is evident on the darker plates of the last three abdominal segments.

In dark specimens, the dorsum of the abdomen is just as dark and smoky (almost blackish) as the thorax, with a cream or light amber broken median line. The sides of tergite 3 have large pale ivory patches. The sides of tergites 4 to 6 are tinted light brown, with a pinkish undertone. The side blotches of tergites 7 and 8 have grown into dark saddles interrupted dorsally by the pale midline and laterally by an ivory border separating them from the laterotergal lobes. Tergite 9 is faded to golden brown, and is sometimes lighter than the rest of the abdomen.

Occasional intermediates between the two color phases have tawny abdominal segments transversely striped to varying degrees of darkness. Kelson (1964) described the abdomen of all the instar 5 nymphs, of the related, undescribed species, as white or nearly white, except segments 7 to 9, which were black.

The laterotergites of this instar are broad and subsquare, expanding like fins from the membranous pleuron, and flatly enclosing the entire caudal length of the sternal chamber up to the fleshy shelf and gasketlike nipple of segment 3. Flexing of the abdomen pulls these plates open and apart. The nipple, prominent in the earlier instars, is reduced to a small nodule in this instar.

The female genitalic lobes are proportionally 2X longer than in the previous instar, darker brown and more conspicuous, otherwise unchanged. The male lobes have grown, both pairs now resembling Dutchman's breeches, the legs of which spraddle wide apart. They lie on the venter of segment 9.

Those of the female extend across the sternum of both segments 8 and 9.

Adult

Our adult females average 9.18 mm long (range 8.6 to 10.0 mm); males average 8.23 mm (range 7.6 to 9.2 mm). Both are of uniform coloration, varying from chestnut tan to chestnut brown with age. The abdomen of older males is much darker than that of females—the tergites becoming blackish. Markings are otherwise identical between the sexes.

A creamy white inverted Y is discernible on the dorsum (Fig. 6D) similar to that of *cribrata*, the thin leg of which runs medially from the apex of the head down to the caudal apex of the scutellum, the wide chevron obliquely banding the hemelytra to either side. In *saratogensis*, this marking is more conspicuous, broader, and lance-shaped. Preserved or callow specimens of *canadensis* are more homogeneous brown than when alive or mature, and the Y is inconspicuous.

The frons of *canadensis* is not so bulbous and inflated as that of *cribrata*. In lateral view, the face meets the vertex at an acute angle, the apex of the head tilting upward like a pig's snout. The crown of *canadensis* is long in comparison with the thorax, and the head is wider than the thorax.

The male genitalia of *canadensis* has been diagrammed and discussed in detail by Walley (1928) and by Doering (1941) and will readily distinguish this from other species of *Aphrophora*.

SEASONAL HISTORY AND BEHAVIOR

Egg

Eggs were present from mid-August until mid-May. *Aphrophora canadensis* overwinters in the egg stage among the needle clusters of the current year's terminals. Like those of the Saratoga spittlebug on jack pine (*Pinus banksiana* Lamb.) (Ewan 1961), the eggs of *canadensis* are inserted separately into the fascicle sheath surrounding the base of each needle cluster, oriented parallel to the needles with the black sutured end upward. The egg is not glued or rooted in any way but held secure by the encircling fibers of the fascicle sheath.

Frequently, more than one egg is inserted in a fascicle (Fig. 2). Four branch terminals were examined for eggs in late September 1981. Of the 300 fascicles counted, 30 had eggs, distributed as follows: 19 fascicles had 1 egg, 8 had 2, 2 had 4, and 1 fascicle had 5 eggs.

Hatching

Nymphs hatched between late April and mid-May. A typical individual required 15 minutes to hatch. The black trapdoor broke from the chorion, tilting slowly downward like a tiny drawbridge. Simultaneously, there appeared in the gap an orange bulge pressing upward like a shining balloon, pushing the lid outward as it rose. Soon two small dark eyes became evident, then the folded mouth parts and the sealed appendages, as the creature ascended by slow increments through the top of its blue shell. For 5 minutes it lay on the substrate, arching and writhing its sealed-up looking body, after which the antennae lifted free from the face. Seven minutes later, the legs unfolded. Three minutes more, and the nymph was climbing to its feet, ready to run. The shed skin was hardly noticeable; the appendages seemed simply to separate from the body as if by drying.

Feeding and Spittle Formation

Upon gaining its feet after hatching, a nymph would run out along the length of a needle, dragging its disproportionately long beak between its legs—for in newly hatched nymphs this organ extends ventrally to almost the abdomen's apex. Pausing a little below the tip of the needle on the dorsal surface, the nymph heaved its head back while rearing high on its legs and sank its colossal beak into the needle.

Nymphs cannot form spittle until they have begun feeding. While the nymph sucks, its head pulses actively. Meanwhile, a clear, viscous liquid begins to drool down the slightly elevated abdomen and over the entire insect, accumulating between its legs in the manner described for the pine spittlebug by Speers (1941). To produce bubbles, the nymph then flexes and rears its abdomen (Fig. 1B) against the surface tension of the slime covering it, and dilates the ventral valvelike plates of segment 9. This dilation creates a V-shaped, snorklelike opening, allowing air to enter the sternal chamber.

The valves shut as the tip of the abdomen is pulled back into the liquid. Then, with a sidewise twist of the abdomen, they open again and release a large bubble. The sequence is repeated on the opposite side. This procedure takes place at a fairly rapid rate, back and forth from side to side like a mechanical shuttle, producing bubbles of similar size.

Feeding Sites

Hatchlings do not usually create much spittle, nor do they remain solitary for long. Within a few days to a week after hatching they abandon their initial feeding sites and wander about intermittently until they find another suitable feeding site.

The ripening female cones provide a large and nutritious surface and are favored as feeding sites. As many as 100 individuals may gather on one cone. If cones are absent from a branch, smaller aggregations form in the axils of needle clusters, especially on current-year terminals. Where two or three spitmakers have joined company, others will congregate on discovering the frothy oasis. This sharing doubtless has survival value by reducing the individual effort needed to maintain a large canopy of foam. Many nymphs become motionless while feeding, with their tails sticking through the froth and ventral vent passively open to the air as if to breathe.

The numbers of nymphs aggregated at a feeding site decreased as the nymphs molted and grew, due probably to crowding and subsequent migration. By instar 5, a few spittle masses contained only one or two nymphs. Younger aggregations were limited to the terminal portions of a tree while older instars, especially the 5th, were sometimes found feeding and foaming along the older, woodier (third to fifth year) portions of branches, if needles were retained there. Such nymphs fed adjacent to the base of a needle cluster, frequently in contact with it, and always oriented head downward with respect to gravity. In contrast, nymphs on cones were arranged every which way, top and bottom, over the cobbled surface, wallowing in one another's spittle. Nymphs congregated on the more sheltered base and undersurface of cones only when their numbers were too small to maintain a large canopy of foam against the summer sun. More typically, the nymphs were assembled over the entire cone, collectively exuding a long white beard of spittle (Fig. 4) dripping to the branches below.

Seasonal Occurrence of Nymphal Stages

Instar 1 nymphs were present in 1981 on trees beginning the last week in April through 22 May; instar 2 nymphs were collected from 5 May through 12 June; instar 3 between 4 June and 22 June. Instar 4 specimens were present in samples between 12 June and 9 July. The instar 5 appeared by the end of June. Spittle masses diminished after mid-July, when nymphs began transforming to adults, but persisted through the first week of August.

Adult Emergence and Behavior

At the end of instar 5, the nymphs left the foam and climbed along pine needles to perch near the apex and shed their final exuviae (Fig. 5). Hanging with legs wrapped around the needle, they glued themselves in place by letting their abdomen dry against the perch. After swelling their thorax for several minutes, the midline of the dorsum split lengthwise. The pale, waxen-appearing imago emerged partway and hung from the exuviae by its abdomen, head downward and back concavely arched, the legs folded. The wings were mere buds at this time. The imago remained in this position for several minutes; then, stirring its legs restlessly, caught hold of the exuviae and drew itself forward to extract the abdomen. Still gripping the exuviae, the imago continued to hang from below, back arched, the four waxen white wings held apart and slowly unfurling (Fig. 6A). When the wings were expanded and dry, the adult stirred from its

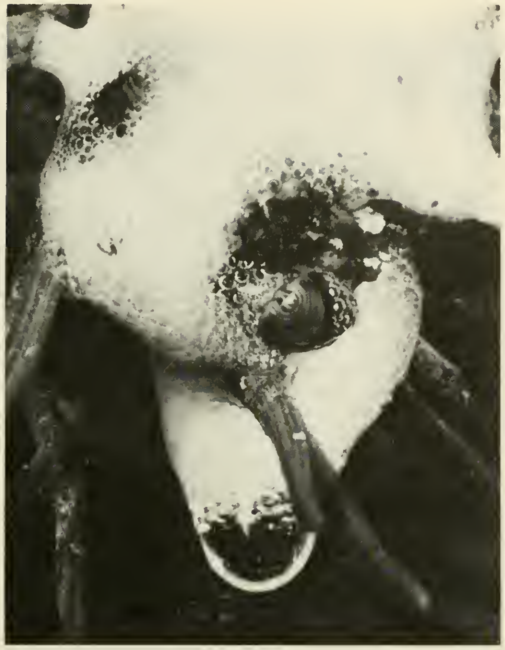

Fig. 4. Commonly, spittle on cones was so massive as to drool drops of liquid. Caudal end of mature nymph is visible at right of center.

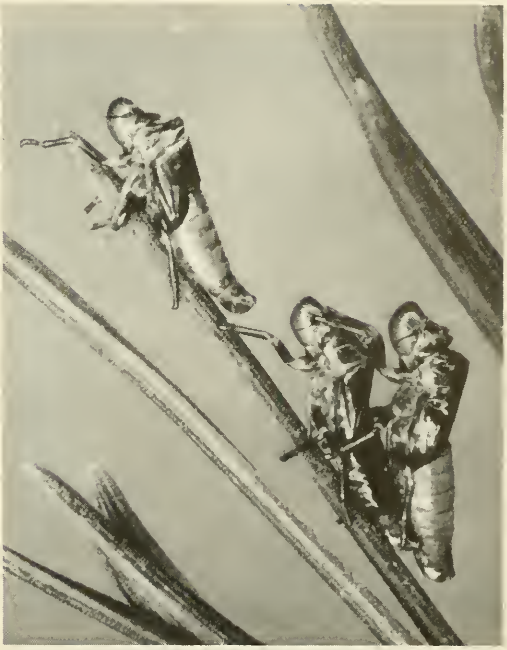

Fig. 5. Exuivae of instar 5 nymphs attached to pine needles.

arched posture, oriented the wings horizontally by shaking them, and folded them shut over its back. All of this required about 30 minutes, at which time the adult was still pale yellowish tan with salmon eyes and ivory wings (Fig. 6C). Mature coloration (Fig. 6D) was attained within a few hours.

Some newly transformed adults roamed freely among the plants, but most preferred the cooler, more shaded portions. Within a few days after ecdysis they began congregating along the terminals to feed, becoming especially active in the late afternoon, when the trees were shaded. As many as 12 adults were counted on the distal 8 inches of a branch.

Adults appeared to feed on the needles as well as on the woody tissues. The brush of needles surrounding the sticky apical bud of a branch was a favorite feeding site. Hoppers often arranged themselves in a ring around the bud, perching on the upper surface of the needles, one per fascicle, facing outward from the branch. Others farther down the limb perched on the needles or crouched against the bark between the fascicles, always oriented with head toward the end of the branch.

While feeding, the hoppers frequently stood motionless with the head and body tilted at an angle of about 30 degrees above the substrate, looking very alert. Positioned thus, they strongly resembled in both shape and coloration the tiny, reddish brown current-year buds. Older and browner specimens were practically invisible against the reticulated scaly surface of the branch, the thin white chevron on their wings matching the onionskinlike fibers of the surrounding fascicles.

When alarmed, the camouflaged hoppers catapulted themselves into the air with remarkable force, making a sharp, snapping sound as they sprang. Girault (1904) likewise noted that pine spittlebugs made "a sound similar to that of a steel spring when suddenly loosened."

Although adult hoppers do not manufacture spit oases, they do secrete honeydew, droplets of which are ejected periodically in rapid-fire bursts, cascading downward in a series of glistening streamers. The hoppers feed and fire droplets throughout the day and night and during copulation, similar to *cribrata* (Speers 1941).

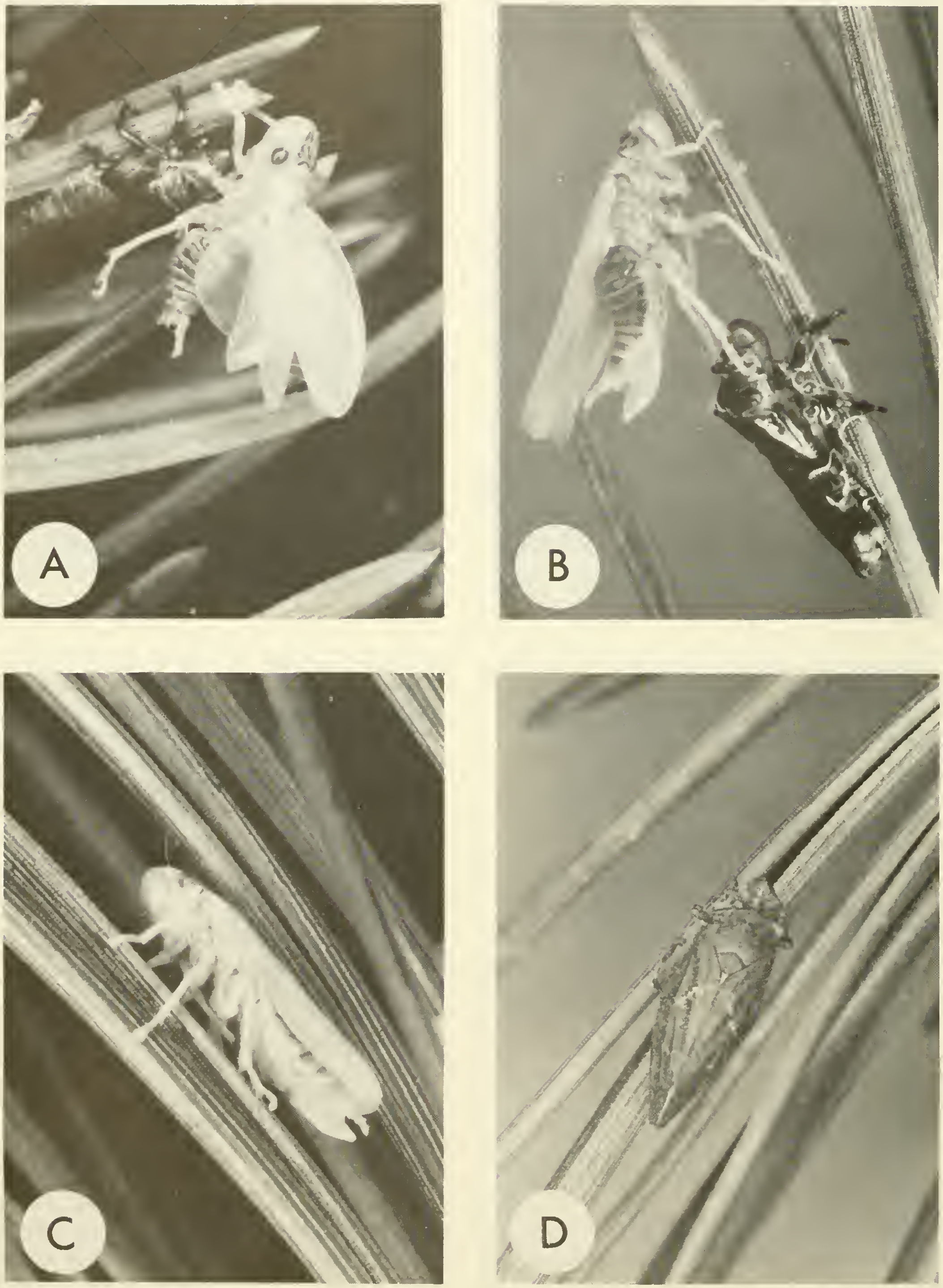

Fig. 6. A, B, C, stages during transformation to adult; D, mature adult with characteristic white chevron wing marking.

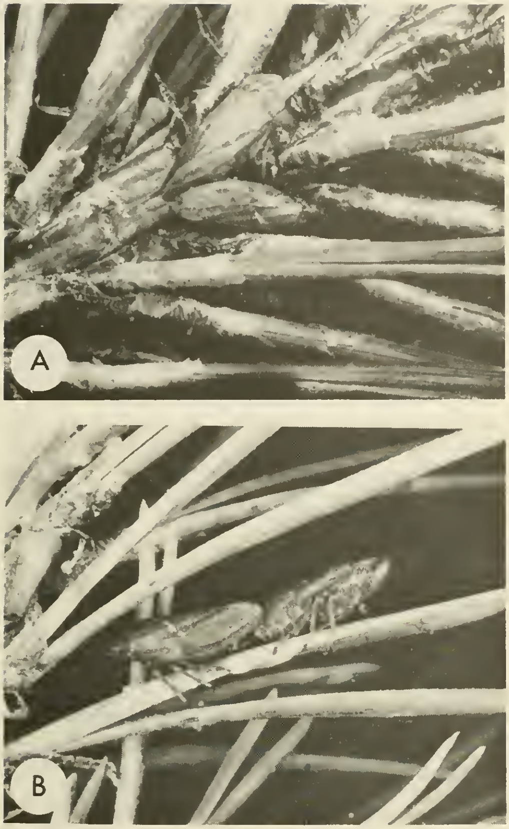

Fig. 7. Most adults assumed a V-stance (A) while mating; others lined up end-to-end (B).

Mating

Copulating pairs were first observed 3 August at 5:00 p.m. Previously, we had searched for paired hoppers only in the morning, finding none. Most couples were engaged side by side, in a V position, their heads pointed toward the end of the branch (Fig. 7A). Some partners also assumed the mating stance described for *cribrata* by Speers (1941) and Girault (1904). In this stance the pair faced away from each other (Fig. 7B), tails overlapping approximately three caudal segments, and the male partner always faced down the branch toward the stem.

The male approached the stationary female by backing tail-first into position. After making contact, copulation ensued. Sometimes they remained thus, facing opposite directions up and down the branch. But more frequently the male pivoted around on his partner until both faced up the branch, side by side.

Copulation lasted several hours, beginning in the afternoon. The partners fed while so engaged. If a male was purposely disturbed by careful poking, he immediately disengaged. Similarly disturbed females were unable to detach from their smaller mates, and often dragged them around helplessly for several minutes.

The hoppers mated until the end of September. Adults survived several weeks of intermittent frost and were last seen 21 October.

ACKNOWLEDGMENTS

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LITERATURE CITED

CRITCHFIELD, W. B., AND E. L. LITTLE, JR. 1966. Geographic distribution of the pines of the world. USDA For. Serv. Misc. Publ. 991. 97 pp.

DOERING, K. C. 1941. A revision of two genera of North American Cercopidae (Homoptera). J. Kansas Entomol. Soc. 14:102–134.

EWAN, H. G. 1961. The Saratoga spittlebug: a destructive pest in red pine plantations. USDA For. Serv. Tech. Bull. 250. 52 pp.

GIRAULT, A. A. 1904. Miscellaneous notes on *Aphrophora parallela*. Canadian Entomol. 36:44–48.

Hamilton, K. G. A. 1982. Taxonomic changes in *Aphrophora* (Rhynchota: Homoptera: Cercopidae). Canadian Entomol. 114:1185–1189.

Hedlin, A. F., H. O. Yates III, D. Cibrian Tovar, B. H. Ebel, T. W. Koerger, and E. P. Merkel. 1980. Cone and seed insects of North American conifers. Canada For. Serv.; USDA For. Serv.; Secretaria de Agricultura y Recursos Hidraulicos, Mexico. Printed in Canada. 122 pp.

Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. USDA For. Serv. Agric. Handbook No. 3856. 658 pp.

Kelson, W. E. 1964. The biology of *Aphrophora permutata* and some observations on *Aphrophora canadensis* attacking Monterey pine in California (Homoptera: Cercopidae). Pan-Pacific Entomol. 40(3):135–146.

Speers, C. F. 1941. The pine spittlebug (*Aphrophora parallela* Say). Bull. New York State Coll. Forest. Tech. Pub. 54, Vol. 14, No. 2a. 65 pp.

Walley, G. S. 1928. The genus *Aphrophora* in America north of Mexico (Cercopidae, Hemipt.). Canadian Entomol. 60:184–192.

Wilson, L. F. 1978. Saratoga spittlebug. USDA For. Serv. For. Ins. and Dis. Leafl. 3. 4 pp.

SEED AND CONE INSECTS ASSOCIATED WITH *PINUS MONOPHYLLA* IN THE RAFT RIVER MOUNTAINS, UTAH

Michael J. Jenkins[1]

Abstract.— Dissection and rearing studies of second-year cones disclosed six species of insects associated with the seeds and cones of singleleaf pinyon pine during the spring and summer of 1976. Those most commonly encountered were: *Dioryctria* sp. probably *albovittella* Hulst, *Conophthorus monophyllae* Hopkins, and *Pineus coloradensis* Gillette. The three remaining species were of lesser importance. These included the gall midge, *Asynapta* sp., a minor cone pest and two parasites, one of *C. monophyllae*, *Acerocephala atroviolacea* Crawford, and an unidentified parasite of *Dioryctria*, of the family Ichneumonidae.

Dioryctria sp. probably *albovittella* was regarded as the major insect destroying cones and seeds of *P. monophylla* in this study. During the growing season it attained a maximum level of 29% infestation. *Conophthorus monophyllae* occurred less frequently in this study, but probably has a higher potential for destruction in years of poor cone crops or high cone beetle populations. *Pineus coloradensis* caused negligible damage to seeds and cones, but was encountered frequently. Early in the growing season it infested a maximum of 38% of the cones.

Insects are probably the most important biotic agents reducing fruit and seed production of trees and shrubs (USDA 1974). This study was conducted to determine those seed and cone insects attacking the cones of the singleleaf pinyon pine, *Pinus monophylla* Torrey & Fremont.

Singleleaf pinyon pine is a member of a group of closely related pines occupying vast acreages in the semiarid regions of the southwestern United States and Mexico (Critchfield and Little 1966). It can form pure, open forests, or, more commonly, grows in association with the Utah juniper, *Juniperus osteosperma* (Torrey) Little, in the characteristic pinyon-juniper woodland (Harlow, Harrar, and White 1979). Pinyon-juniper woodlands cover over 75,000 square miles of the southwestern United States (Lanner 1975), occupying more area in the Intermountain Region than all other forest cover types combined (Cronquist et al. 1972).

Little commercial value has been placed on the pinyon pines for timber products, but the seeds of these pines have been harvested for centuries by American Indians as a valuable food supply (Lanner 1981). Various forms of wildlife depend upon pine nuts for survival, among them many birds and rodents. In good seed years, Indians of the Southwest have collected and sold a million dollars worth of pine nuts. Pinyon timber has also been used for fence posts, mine props, and fuel wood, and pinyons serve as excellent Christmas trees (Johnson 1970).

Since little value is placed on pinyon pines for timber products, there have been few studies describing the insects associated with them. This study was conducted to identify: the major seed and cone insects present on singleleaf pinyon pine, to determine their relative abundance, and to briefly describe their life cycles.

Methods

Study Area

The study area was a 530-hectare singleleaf pinyon–Utah juniper woodland in northwestern Utah's Raft River Mountains at an elevation of 1900 to 2300 m.

Quarter-hectare plots were used to determine the relative number of pinyon pines and junipers. There was an average of 178 pinyon pines and 72 junipers per hectare.

The understory vegetation consisted of big sagebrush, *Artemisia tridentata* Nutt., *Opuntia* cactus, and a variety of grasses and forbs. Toward the western boundary of the stand was an increase in curlleaf mountain mahogany, *Cercocarpus ledifolius* Nutt.

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Sampling

A permanent plot center was selected in a part of the stand found to be typical in terms of overstory density and composition.

Ten sampling dates were scheduled beginning in mid-April and continuing into October at two- to three-week intervals. The permanent plot center was used as a starting point for each collection. Prior to each collection date, a direction was randomly selected and traveled to collect the sample. Any tree falling partly or entirely on the line could be sampled. The restrictions to sampling were that not more than 10% of the sample could come from any one tree and that all cones collected came from unshaded branches of nearly average trees on average sites. Collections were made using a pole pruner and consisted of 100 cones per collection date.

Analysis of the Sample

The sample was returned to the laboratory and cones were grouped based on the exterior appearance of insect damage. Cones showing no exterior evidence of insect activity were also grouped together. Half the cones in the sample were dissected using a cone cutter and the remainder were placed in rearing chambers. Immature insects dissected from cones were recorded and preserved in 70% EtOH for identification by specialists. Rearing of early samples was not attempted, as the small cones dried too rapidly.

Once cones reached sufficient size, emphasis was shifted from dissection to rearing, to obtain adult specimens for identification. Dissection of damaged and normal cones continued using a smaller number of cones to characterize types of damage and to assess the number of individuals attacking a given cone.

Rearing began in July with collection number III. Cones were separated and grouped based on external damage, placed in containers covered with cheesecloth and left at room temperature (18–22 C) (Ebel 1959). Insect specimens collected from rearing chambers, whether adult or immature, were sent to specialists for identification.

Results

The insect species collected and identified from seeds and cones of singleleaf pinyon are listed in Table 1. Following are discussions of the nature of the damage caused by each insect and descriptions of their life histories.

Conophthorus monophyllae Hopkins (Coleoptera: Scolytidae)

Pine cones that dry and wither before they are half grown are said to be "blighted." The usual cause of blighting is pine cone beetle damage by the genus *Conophthorus* Hopk. (Keen 1958). Species in this genus were believed by Hopkins (1915) to be specific to a particular member of the genus *Pinus*. *Conophthorus monophyllae* is a unique species consistently associated with *P. monophylla* (Wood 1982: 984).

The range of *C. monophyllae* would be expected to correspond to that of *P. monophylla*, with the beetle being found wherever the singleleaf pinyon pine occurs. However, collection of *C. monophyllae* in the study area represented an extension of its known range by more than 200 miles (Wood 1982).

Table 1. Insects associated with seeds and cones of *Pinus monophylla* in the Raft River Mountains.

Order	Family	Scientific name
Coleoptera	Scolytidae	*Conophthorus monophyllae* Hopkins
Lepidoptera	Pyralidae	*Dioryctria* sp. probably *albovittella* Hulst *Dioryctria* sp. probably *abietella* D. & S.
Homoptera	Adelgidae	*Pineus coloradensis* Gillette
Diptera	Cecidomyiidae	*Asynapta* sp. Loew
Hymenoptera	Pteromalidae Ichneumonidae	*Acerocephala atroviolacea* Crawford One unidentified species

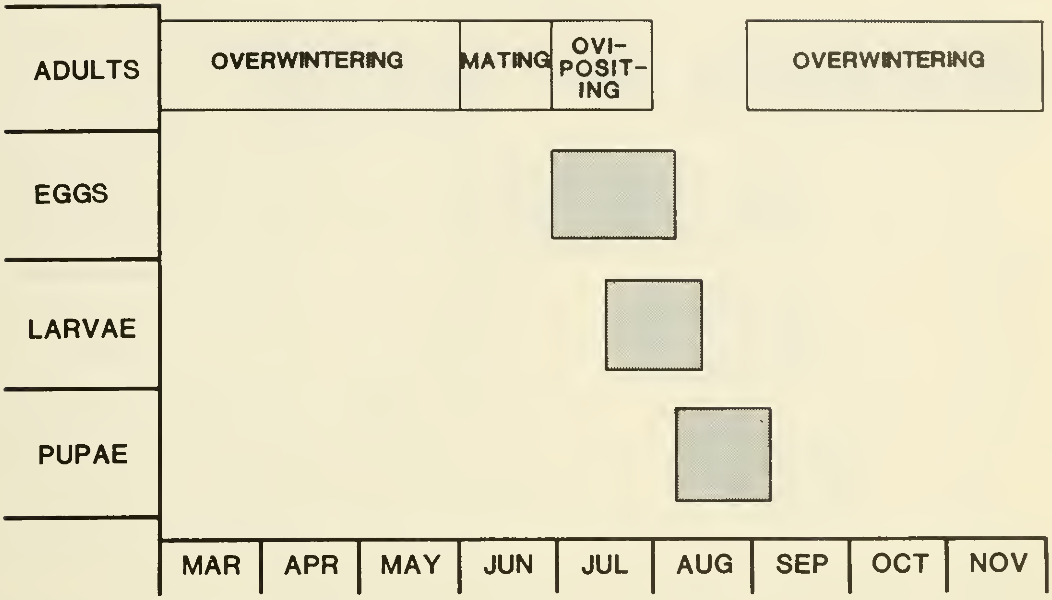

Fig. 1. Life history of *C. monophyllae* showing life cycle stages and their occurrence during the growing season. Adapted from Keen (1958) and field observations.

Life history. Mating occurs in late spring or early summer, and by early July the female beetle lays her eggs in the second-year cones. The cone is killed by the attack of the adult beetle, as she bores a tunnel into the base of the cone and up its central axis, depositing eggs in niches to the sides of the tunnel. The egg niches and tunnel are packed with frass. The first larvae were observed within the cone by mid-July. The larvae feed on the seeds and cone scales, honeycombing the interior of the cone. Pupation occurs in mid- to late August with the adult emerging two to three weeks later. The newly emerged adults overwinter in the dead cone and feed on the drying tissue. They become dormant during the winter and emerge the following spring (Fig. 1). The exact date of emergence will vary with springtime temperatures. There is one generation per year.

Damage. Cones that were attacked by *C. monophyllae* the previous year were readily identifiable by the numerous emergence holes in the cone scales. Previously attacked cones may either remain on the tree or fall to the ground. Old injury was easily found in the study area, although specific counts were not attempted.

Cones that were attacked early in the current growing season were hard, brown, and wrinkled by the end of the season. The entrance hole made by the adult female was visible near the base of the cone, with very little resin or frass present around the hole.

Cones that were attacked later in the season opened prematurely and had an entrance hole near the base. The interior contained larvae, pupae, or adults. Larvae boring in nearly mature cones preferred the individual seeds and were most commonly encountered there with only one larva feeding in any given seed. They reduced the interior of the seed to strips of elongate frass and pupated within the cone. The adult emerged the following spring by way of a hole bored through the cone scale. During the study year, the number of cones attacked by *Conophthorus* did not exceed 11% (Table 2, Fig. 2).

Dioryctria probably *albovittella* Hulst (Lepidoptera: Pyralidae)

Problems were encountered with the identification of the species of *Dioryctria* involved. A long series of larvae was identified by D. M. Weisman as probably being *D. albovittella* Hulst. However, adults that were obtained from rearing chambers containing cones infested with *Dioryctria* sp. appeared to Weisman and D. C. Ferguson to be *D. abietella* D. & S. Weisman and Ferguson

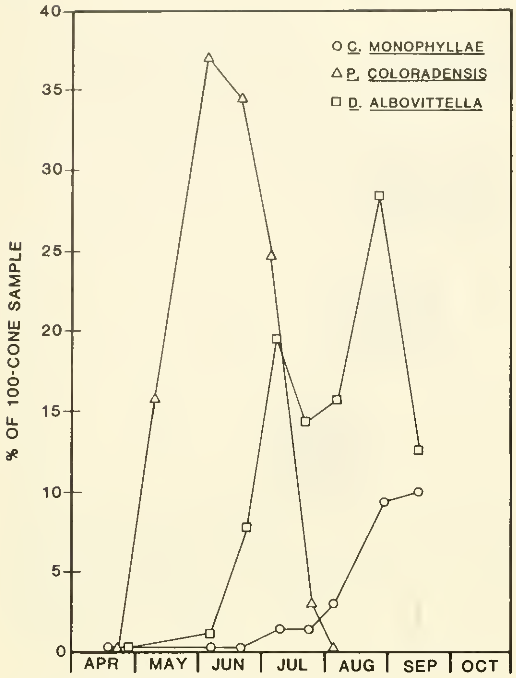

Fig. 2. Percentage of cones attacked by major insect species at various times during the study.

(pers. comm.) believed one of two possible situations existed: the first, and most likely, was a mixed population consisting of *D. albovittella* and a few *D. abietella*. If this was the case, it appeared that the rearing techniques used here might have selected for *D. abietella*. The second possibility was that a new species was involved, which Weisman considered to be unlikely.

The caterpillars of this species of moth fed on the bracts, scales, and seeds of second-year cones, causing blighting, deformity, and sometimes death of the entire cone. Usually a variable percentage of seeds was destroyed and the remainder were unaffected. The activity of these caterpillars was easily identifiable by a large hole in the cone's exterior covered by frass, webbing, and resin (Keen 1958).

Dioryctria albovittella is specific to cones of *P. monophylla* and should be encountered throughout the range of the singleleaf pinyon. The first recorded rearing of *D. albovittella* was from collections made near Topaz Lake, Nevada, in 1939 (Keen 1958). It has a wide host range, affecting a number of coniferous species.

Life history. This species overwinters as eggs laid by females on twigs. The eggs hatch in early spring, and larvae are active in the cones from June through September. Pupae form in sparsely lined pupal cells in July, August, and September. Adults emerge from the cones in August and September. Mating occurs during this period and eggs are again deposited on twigs (Keen 1958; Fig. 3).

Damage. The first larvae were encountered in early July, burrowing in young second-year cones. The activity was evident from a hole covered by frass, webbing, and resin in the exterior of the cone. The frass existed as large spheres, differing from that of *C. monophyllae* described earlier. The gallery within the cone was packed with frass and resin; the tissue immediately adjacent to the gallery dried and turned brown. The caterpillars fed without discrimination on scales and seeds, with only one caterpillar active within any given cone. Small cones attacked early in the season were totally destroyed, but larger cones attacked later showed only partial destruction and could bear some normal seeds and open some scales at maturity (Little 1944).

The first pupae were observed in late July in dry cones. It appeared that the larvae fed for a determinate length of time and then pupated within the drying cone. Pupae and lar-

Table 2. Percentage of the 100-cone sample collected on each of the dates shown and attacked by the three most important insect species. Data are shown for various collection dates in 1976. See also Figure 2.

	Collection date								
Species	Apr 18	May 8	Jun 3	Jun 20	Jul 6	Jul 21	Aug 3	Aug 23	Sep 13
D. albovittella	0	0	1	8	20	15	16	29	13
C. monophyllae	0	0	0	0	1	1	3	10	11
P. coloradensis	0	16	38	34	25	3	0	0	0

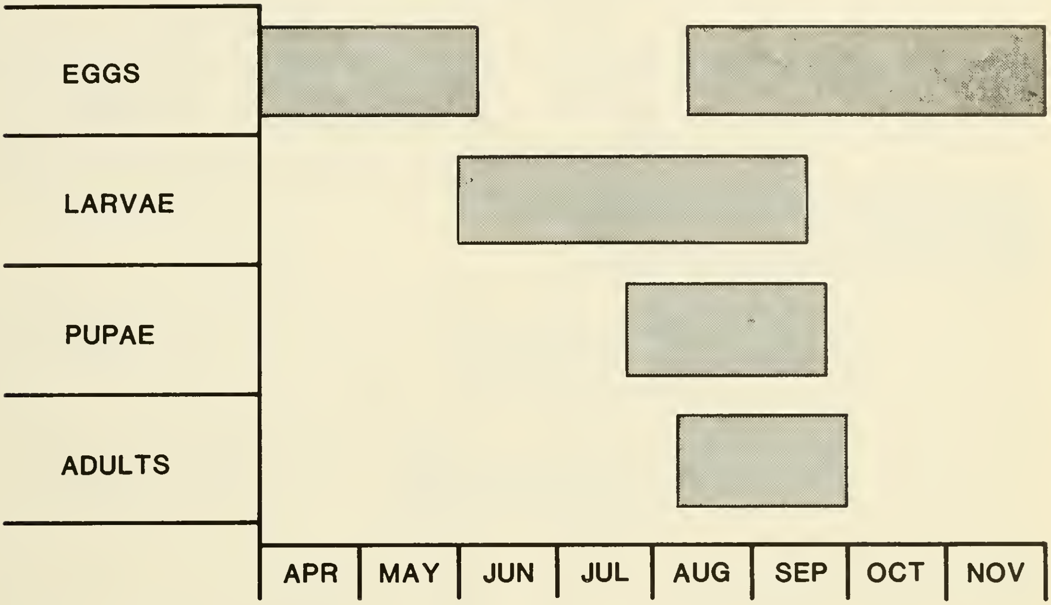

Fig. 3. Life history of *D. albovittella*. Adapted from Keen (1958) and field observations.

vae were collected until the latter part of August.

The percentage of cones attacked ranged from 1% on 3 June to 29% on 23 August. After this time, the incidence of attack dropped off (Figure 2; Table 2).

Pineus coloradensis Gillette (Homoptera: Phylloxeridae)

Species within the genus *Pineus* form dense mats of wax, often covered by mold, on twigs of ponderosa, Jeffrey, lodgepole, sugar, pinyon, white, and singleaf pinyon pines (Keen 1952). The damage caused by this genus is usually minor, although it can cause unsightliness on ornamentals. A species in the same subfamily, *Adelges cooleyi* Gillette, causes the familiar shoot tip gall seen locally and elsewhere on *Picea pungens* Engelm.

Description. This species is widely distributed throughout the western United States.

Life history. "Few groups of insects have the complexities of life cycle or the varieties of form which are exhibited by the members of the subfamily Adelginae (Annand 1928)." Two different species of conifers are necessary to complete the life cycle. For most members in the genus *Pineus* the primary host is *Picea* (Doane et al. 1936). However, for *P. coloradensis* no alternate host is known. Throughout much of the range of *P. coloradensis*, including the study area, spruces did not occur in large numbers and it is doubtful that the alternate host of this species was spruce. Either another as yet unidentified alternate host existed or the alate forms that migrate to this host failed to become established (Annand 1928).

Several generations, usually five, occur in the life cycle of *Pineus*. Four of the five generations are female only, produced parthenogenetically. Males are produced in the fifth generation (Doane et al. 1936).

Early in the summer, winged females emerged from the primary host and migrated to the secondary host, *P. monophylla* in this case. The first observation of *P. coloradensis* on the cones of *P. monophylla* was made on 8 May. The reddish females established themselves in the crevices between cone scales and secreted a waxy coating. Beneath this wax, the female laid eggs and the eggs hatched into nymphs that fed on the resins of the young cones. There was only one female beneath each wax mass, although many females could become established on a given cone. Thirty-eight percent of the cones in the sample taken on 3 June showed this activity (Table 2). This figure dropped off very rapidly during June and July, and no observations were made of *P. coloradensis* after 21 July (Fig. 2). Development into alate adults and subsequent dispersion apparently occurred quite rapidly, resulting in this marked decrease in the insect population present on the cones.

Damage. The secretion of wax and ovipositing by females of *P. coloradensis* did no apparent damage to the cones of *P. monophylla* internally or externally. Observations made on cones displaying *P. coloradensis* showed subsequent normal development during the time the insect was present and after it dispersed. Adult females can lay up to 100 eggs, and it has been noted that the feeding activity of immatures on new growth can be harmful, especially to young trees, if the insect is present in abundance (Doane et al. 1936). In the introduction to this section, it was noted that an unsightly condition on ornamentals can result from the presence of species in this and related genera.

Previous reports of this insect have restricted its occurrence to needles and twigs. This study demonstrated that cones represented an important additional habitat.

Other Insects

Three additional insect species were obtained from the cone samples. One was a cone pest identified only to the genus *Asynapta.* The two remaining insects were parasites, one of *D. albovittella* and the other of *C. monophyllae.* The gall midge genus *Asynapta* (Diptera Cecidomyiidae) (USDA 1965) is capable of causing destruction of first-year cones (Felt 1935). First-year cones were not considered in this study, and *Asynapta* sp. was collected from a sample of second-year cones. The limited publications, isolated occurrence, and the fact that only immatures were obtained made it impossible to determine the life cycle or specific identification.

Two parasites were identified. One was an adult specimen of *Acerocephala atroviolacea* Crawford that develops on larvae and pupae of Scolytidae (Clausen 1940), in this case *C. monophyllae.* It has previously been reared from *C. edulis*-infested cones of *P. edulis* at Ute Pass, Colorado, and Las Vegas, New Mexico (Gahan 1946). The other parasite was a member of the Ichneumonidae, which are common parasites of caterpillars. The one reared out in this study was associated with *Dioryctria* sp., but its positive identification was not possible due to the previously discussed problems in identifying the *Dioryctria* sp. found in this study.

Discussion

Very few insect species have been described in association with *P. monophylla.* From the literature, three species have been listed as the most important pests of second-year singleleaf pinyon pine cones. These are, according to Keen (1958), *Conophthorus monophyllae*, *Dioryctria albovittella*, and *Eucosma bobana.* Little (1943, 1944) also emphasized the importance of the genera *Conophthorus* and *Dioryctria* on *P. edulis.* Keen and Little mentioned the activity of unidentified gall midges of the family Cecidomyiidae as having an impact on cone crops, especially on first-year cones.

In this study, *D.* probably *albovittella* and *C. monophyllae* were the most serious pests reducing seed production in *P. monophylla.* The adelgid, *Pineus coloradensis*, was of widespread occurrence, but caused little damage in the study area. The cecidomyiid of the genus *Asynapta* was encountered only once and was considered to be of minor importance. *E. bobana* was not collected in the study area.

Dioryctria probably *albovittella* was widespread and regarded as the most damaging insect species attacking second-year cones of *P. monophylla.* The caterpillars were present and active in cones throughout much of the growing season, feeding without discrimination on all parts of the cone.

The singleleaf pinyon cone beetle, *C. monophyllae,* has a high potential for reducing seed production. Large numbers of offspring developed in and emerged from a single cone. In this study, no cone found to be attacked by cone beetles contained any normal seeds. The incidence of attack in the study area, however, was low, though typical *Conophthorus* populations do increase during years of heavy cone production, then affect a large percentage of cones the following year (Forcella 1980). One significant outcome of

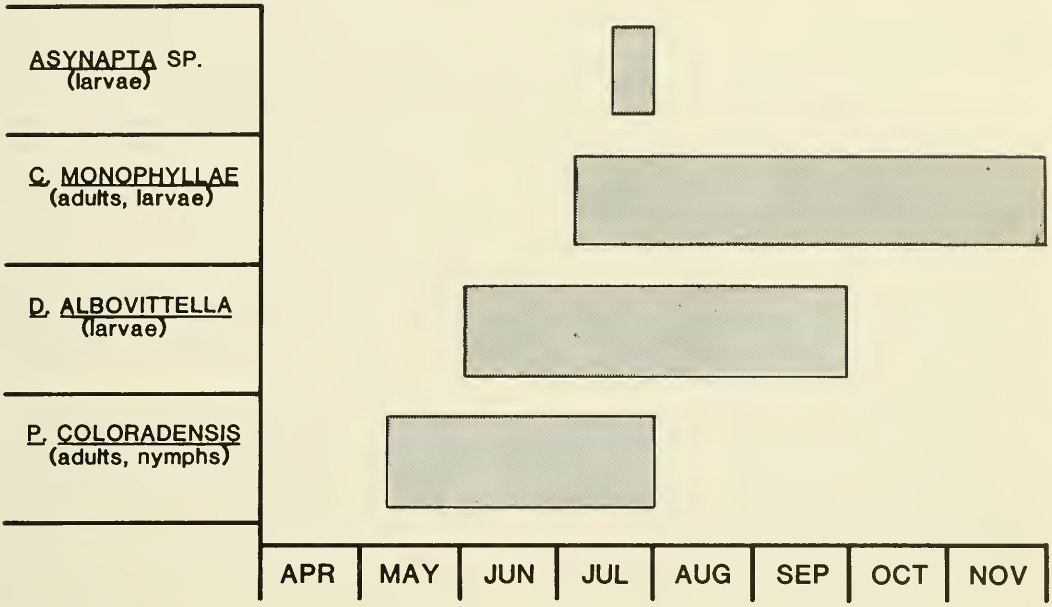

Fig. 4. Time of activity of various insect species during the growing season.

this study was the extension of the known range of *C. monophyllae* by 200 miles.

Pineus coloradensis is a species of minor economic importance. Its collection and identification in this study was of value because it represents the first recorded observation of this insect species on *P. monophylla*. In addition, *P. coloradensis* was not previously reported. Further research on this species in the study area would be valuable in determining the primary host and in obtaining a more thorough understanding of its complex life cycle.

Larvae of the gall midge, *Asynapta* sp., were encountered only once in this study. Keen and Little reported unidentified gall midges of the same family (Cecidomyiidae) as being the most important insects damaging first-year cones, but this study apparently represents the first report of *Asynapta* sp. in the western United States. Because no adults were obtained, identification to the species level was not possible.

Two parasitic insects were also contained in this study. *Acerocephala atroviolacea* was parasitic on *C. monophyllae*. The other parasite attacked *D. albovittella* and could be identified only to the family level. Neither was obtained in abundance and was not believed to be effective in reducing cone beetle or cone worm populations during the year of the study.

There was some correlation between the time of attack by the major insect species and the seasonal history of the cone. *Pineus coloradensis* was most active on the cones during the early part of the season. At this time, the cones were producing the most resin for the adults and immatures to feed upon. *D. albovittella* was active during the early and middle portion of the growing season, when the cones were growing rapidly and were very succulent. Caterpillars can feed on any of the cone tissues during this time. However, by late August, when the cones were reaching maturity, the occurrence of *D.* probably *albovittella* declined sharply. *Conophthorus monophyllae* preferred to feed on the individual seeds within a cone. It did not become active until the cone had matured to the point that individual seeds were evident (Fig. 4).

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LITERATURE CITED

ANNAND, P. N. 1928. A contribution toward a monograph of the Adelginae (Phylloxeridae) of North America. Stanford Univ. Pub. Biol. Sci. 6:1–146.

CLAUSEN, C. P. 1940. Entomophagous insects. McGraw-Hill Book Co., Inc., New York and London. 688 p.

CRITCHFIELD, W. B., AND E. L. LITTLE. 1966. Geographic distribution of the pines of the world. USDA, Forest Service Misc. Publ. 991. 97 pp.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora: vascular plants of the Intermountain West, USA. Vol. 1. Hafner Publishing Co., New York and London. 269 pp.

DOANE, R. W., E. C. VAN DYKE, W. J. CHAMBERLIN, AND H. E. BURKE. 1936. Forest insects. McGraw-Hill Book Co., Inc., New York. 463 pp.

EBEL, B. H. 1959. Laboratory rearing of the pine cone insect *Dioryctria abietella* (D. & S.). J. Econ. Entomol. 52;561–564.

FELT, E. P. 1935. A gall midge on pine cones. J. New York Entomol. Soc. 43:48–49.

FORCELLA, F. 1980. Cone predation by pinyon cone beetle (*Conophthorus edulis*): dependency on frequency and magnitude of cone production. Amer. Natur. 11:594–598.

GAHAN, A. B. 1946. Review of some chalcidoid genera related to *Cerocephala* Westwood. Proc. U.S. Nat. Mus. 96:370.

HARLOW, W. H., E. S. HARRAR, AND F. M. WHITE. 1979. Textbook of dendrology. McGraw-Hill Book Co., New York. 510 pp.

HOPKINS, A. D. 1915. A new genus of scolytoid beetle. J. Washington Acad. Sci. 5:429–433.

JOHNSON, C. M. 1970. Common native trees of Utah. Agr. Expt. Sta., Coop. Ext. Service, College of Natural Resources, Utah State Univ., Logan, Utah. 109 pp.

KEEN, F. P. 1952. Insect enemies of western forests. USDA Misc. Publ. 173. 280 pp.

______. 1958. Cone and seed insects of western forest trees. USDA Tech. Bull. 1169. 168 pp.

LANNER, R. M. 1975. Pinyon pines and junipers of the southwestern woodlands. *In* The pinyon-juniper ecosystem: a symposium. Utah Agr. Expt. Station, Logan. 194 pp.

______. 1981. The piñon pine. A natural and cultural history. Univ. of Nevada Press, Reno. 208 pp.

LITTLE, E. L. 1943. Common insects on pinyon (*P. edulis*). J. New York Entomol. Soc. 51:239–253.

______. 1944. Destructive insects on pinyon (*P. edulis*). USDA, Forest Service, Rocky Mt. Forest and Range Expt. Sta. Res. Note 110. 4 pp.

U.S. DEPARTMENT OF AGRICULTURE, AGRICULTURE RESEARCH SERVICE. 1965. A catalog of Diptera of America north of Mexico. Agricultural Handbook 276. 169 pp.

U.S. DEPARTMENT OF AGRICULTURE, FOREST SERVICE. 1974. Seeds of woody plants of the United States. Agricultural Handbook 450. 883 pp.

WOOD, S. L. 1982. The bark and ambrosia beetles of north and central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat. Memoirs, No. 6. 1359 pp.

BRISTLECONE PINE AND CLARK'S NUTCRACKER: PROBABLE INTERACTION IN THE WHITE MOUNTAINS, CALIFORNIA

Ronald M. Lanner[1], Harry E. Hutchins[1], and Harriette A. Lanner[1]

Abstract.— Many bristlecone pines in the White Mountains, California, are members of multistem clumps. We propose that these clumps have arisen by multiple germinations from seed caches of Clark's Nutcracker, as occurs in several other pine species. The commonness of nutcrackers and their caching of singleleaf pinyon seeds in the study area provide supporting evidence. Other vertebrates appear unlikely to be responsible for the stem clumps. Seed burial may be required to establish regeneration on these adverse sites where bristlecone pine attains great longevity.

Clark's Nutcracker (Corvidae: *Nucifraga columbiana* Wilson) disperses seeds and establishes seedlings of Colorado pinyon (*Pinus edulis* Engelm.), singleleaf pinyon (*P. monophylla* Torr. & Frém.), limber pine (*P. flexilis* James), and whitebark pine (*P. albicaulis* Engelm.) (Vander Wall and Balda 1977, Tomback 1978, Lanner and Vander Wall 1980). Nutcrackers remove seeds from cones, hold them temporarily in a sublingual pouch, and subsequently cache them in the soil as a winter and spring food resource. Despite a marked preference for the large wingless seeds of the above-mentioned species, nutcrackers sometimes harvest as well the smaller winged seeds of ponderosa pine (*P. ponderosa* Laws.), Jeffrey pine (*P. jeffreyi* Grev. & Balf.), and even Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) (Giuntoli and Mewaldt 1978, Tomback 1978). Seeds left unretrieved frequently germinate as groups of seedlings that develop into distinctive tree clumps in which the number of stems reflects the number of seeds per cache. High frequencies of multiple stem clumps, as opposed to single stems, characterize limber and whitebark pine, and greatly exceed clumping in winged-seeded conifers not cached by nutcrackers (Lanner 1980). Clark's Nutcracker is the only reliable agent of seed dispersal and seedling establishment of whitebark pine, other animals lacking the capability of serving these functions (Hutchins and Lanner 1982). The similarity of fauna in whitebark and limber pine forests suggests it is the most effective disperser and establisher of limber pine as well.

Great Basin bristlecone pine (*P. longaeva* D. K. Bailey) has relatively small winged seeds (USDA Forest Service 1974). Peattie (1953) reported that nutcrackers harvest seeds of *P. aristata* Engelm., under which name he included what has since been segregated as *P. longaeva*. Vander Wall and Balda (1977) stated that *P. aristata* seeds were eaten by nutcrackers, but probably not stored unless local pinyon and limber pine seed crops had failed. In this paper we present evidence that nutcrackers not only eat bristlecone pine seeds, but they also store them in the soil, thus causing establishment of seedlings.

Methods

The study area is the Ancient Bristlecone Pine Forest, a dedicated botanical area within the Inyo National Forest in the White Mountains, California. We made observations 23 July and 30 September–3 October 1982 in the Schulman Memorial Grove (3030–3150 m) and the Patriarch Grove (3425 m). Both areas have substrate of light gray to white dolomitic limestone that frequently forms a pavement of small fragments. Bristlecone pine is the predominant tree species. Limber pine occurs sporadically in both groves but does not reach tree size in the Patriarch Grove. The most common shrubs are of the genera *Artemisia* and *Ribes*, but the ground is mostly bare of vegetation (Fig. 1).

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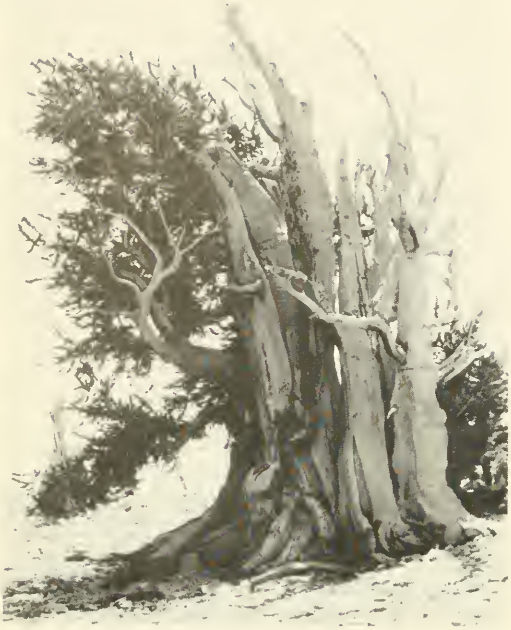

Fig. 1. An ancient bristlecone pine stem clump growing on dolomite in the Patriarch Grove.

Three 20 x 50 m transects were laid out in each grove, through typical forest cover. Data recorded for each tree in each transect were species, diameter class (<1 cm, 1–10 cm, >10 cm at breast height), and number of independent stems in contact at the root collar. The transects sampled east, northeast, west, northwest, and south aspects.

Diurnal vertebrates were identified and counted during 29.25 hr in the Schulman and Patriarch Groves and in a limber pine woodland nearby at 3000 m. A "visit" is an episode in which an individual animal was observed in (bird) or at the base of (mammal) a bristlecone pine tree; or, in the case of the lower woodland, a limber pine tree.

Results

Stem clumps were common among trees of both species and of all diameter classes, at both groves. All the limber pines were members of multistem clumps. Bristlecone pine was more highly clumped in the Patriarch Grove than in the Schulman Grove (Table 1). Though one would intuitively expect larger and therefore older trees to have fewer stems per clump due to attrition, no such relationship was detectable in the data. It is suggested by Forest Service interpretive signs in the Patriarch Grove that the multistem habit of bristlecone pines there is due to the rooting of prostrate branches (i.e., layering); but close examination of clumps disclosed no evidence of such an origin.

In 26.25 hr of animal observations, 11 species of birds and 2 of mammals were observed in or at the base of bristlecone pines. The following species are omitted from Table 2 because they are not considered possible dispersers or establishers of bristlecone pine: White-breasted and Pygmy Nuthatches, Dark-eyed Junco, White-crowned Sparrow, Hairy Woodpecker, Mountain Chickadee, and Common Flicker. None of these species is reported to cache seeds in the soil. Of the remaining 6 animals considered possible dispersers or establishers, nutcrackers made 88% of the visits to bristlecone pines (Table 2). We saw no seeds actually being harvested from cones of bristlecone pine, which were then beginning to open. There was, however, a high level of harvesting activity by nutcrackers on singleleaf pinyons and limber

Table 1. Stem clumping in bristlecone and limber pines on transects in the Ancient Bristlecone Pine Forest, White Mountains, California. Asterisk (°) indicates significant difference between groves (a = .05, Newman-Keuls multiple mean test).

	Schulman Grove		Patriarch Grove	
	Bristlecone	Limber	Bristlecone	Limber
n (trees)	76	5	122	27
n (clumps)[1]	48	2	45	7
trees/clump, x̄ ± s.d.	1.6 ± .9°	2.5[2]	2.7 ± 2.1°	3.9 ± 1.8
trees/clump, range	1–4	2–3	1–11	2–7
percent multi-stem clumps	46	100	69	100

[1] A clump includes single stems as well as multiples.

[2] Insufficient data for S.D. computation.

pines nearby, even though their cones also were mainly closed. On many occasions nutcrackers were seen caching seeds in the study area, but the five caches that were excavated (four in the Patriarch Grove, one in the Schulman Grove) contained only seeds of singleleaf pinyon. Cones of 50 bristlecone pines from each grove showed no damage of the type often caused by nutcrackers (Lanner 1980).

DISCUSSION

The high frequency of stem-clumping among bristlecone pines (46–69%) cannot reasonably be attributed to the generally random seed-rain resulting from wind dispersal. It compares with the following clumping frequencies of wingless-seeded pines known to be dispersed and established by nutcrackers: limber pine in Logan Canyon, Utah, 53–68%; and whitebark pine in Togwotee Pass, Wyoming, 47% (Lanner 1980). These figures are conservative as indices of nutcracker activity because they exclude (a) caches consisting of one seed only and (b) multiseed caches in which only one germinant survives to be counted. Fritts (1969) found 34% of bristlecone pines in his White Mountain quadrats to be multistemmed. The clumping frequency of limber pine in both groves (100%) and the observations of nutcracker activity there conclusively show that nutcrackers cache seeds in the very areas where clumped bristlecones occur. The transport of singleleaf pinyon seeds to high elevations where seedling survival is doubtful has also been noted in Utah (Lanner and Vander Wall 1980). It may have the ultimate effect of selecting genotypes adapted to these high-elevation conditions.

TABLE 2. Frequency of visits by potential seed dispersers in and adjacent to Ancient Bristlecone Pine Forest, White Mountains, California, 30 September–3 October 1982.

	Schulman Grove	Patriarch Grove	Limber Pine Woodland
Observation time, hours	15.5	10.75	3.0
	Visits per hour of observation		
Clark's Nutcracker	7.0	3.7	25.7
Pinyon Jay	0	.2	0
Scrub Jay	.1	0	0
Raven	.1	.2	.7
Chipmunk	0	.6	0
Golden-mantled ground squirrel	.5	0	0

The much greater density of Clark's Nutcracker in both groves, compared to that of other possible dispersers, further supports the hypothesis that nutcrackers establish bristlecone pine seedlings. Pinyon jays are known to cache pinyon pine seeds in groups (Vander Wall and Balda 1981), but their small numbers suggest a minor role here. Scrub jays seldom cache seeds in groups (Vander Wall and Balda 1981), so are unlikely to be responsible for stem clumps. Though ravens, chipmunks, and golden-mantled ground squirrels are possible dispersers, our recent study (Hutchins and Lanner 1982) has shown such a role highly improbable for them. Also, ground squirrels were not seen in the Patriarch Grove, where clumping was most common. The effect of nocturnal rodents was not measured here, but is probably very minor (Abbott and Quink 1970, Hutchins and Lanner 1982).

The texture of the substrate in both groves is morphologically similar to that of a communal caching site described by Lanner and Vander Wall (1980). Though bristlecone pine distribution in the White Mountains has been attributed largely to the moisture-holding qualities of the substrate (Wright and Mooney 1965), it is possible that the cache-site preference of nutcrackers is also a significant factor.

Our inability to observe nutcrackers harvesting and caching bristlecone pine seeds did not surprise us in view of the availability of the larger limber pine and singleleaf pinyon seeds nearby. The nutcrackers obtained these seeds by tearing up the unopened cones, as they often do (Lanner 1980) with these species. Whether they also demolish the hard, bristly, closed cones of bristlecone pine is unknown. We found no such cones on the ground.

Though some investigators have called attention to the fact that the most ancient of the old bristlecone pines are found on the most adverse sites (Schulman 1954, 1958, LaMarche 1969, Wright and Mooney 1965), they have not addressed the question of how seedlings get established on such sites. We suggest that in the White Mountains, Clark's Nutcracker facilitates bristlecone pine establishment by placing seeds in subsoil caches conducive to germination. Caching prevents seeds from being blown away, preyed upon, or becoming desiccated. Significant regeneration of bristlecone pine probably follows years when a good seed crop of this species coincides with poor crops of limber pine and singleleaf pinyon.

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Literature Cited

Abbott, H. G., and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. Ecology 51:271–278.

Fritts, H. C. 1969. Bristlecone pine in the White Mountains of California, growth and ring-width characteristics. Univ. of Arizona Press, Tucson. 44 pp.

Guintoli, M., and L. R. Mewaldt. 1978. Stomach contents of Clark's Nutcrackers collected in western Montana. Auk 95:595–598.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia (Berlin) 55:192–201.

La Marche, V. C. 1969. Environment in relation to age of bristlecone pines. Ecology 50:53–59.

Lanner, R. M. 1980. Avian seed dispersal as a factor in the ecology and evolution of limber and whitebark pines. North American Forest Biology Workshop Proc. 6:15–48. Univ. of Alberta, Edmonton.

Lanner, R. M., and S. B. Vander Wall. 1980. Dispersal of limber pine seed by Clark's Nutcracker. J. Forestry 78:637–639.

Peattie, D. C. 1953. A natural history of western trees. Houghton Mifflin Co., New York.

Schulman, E. 1954. Longevity under adversity in conifers. Science 119:395–399.

Schulman, E. 1958. Bristlecone pine, oldest known living thing. Nat. Geog. Mag. 113:355–372.

Tomback, D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16(1977):123–161.

U.S. Department of Agriculture, Forest Service. 1974. Seeds of woody plants of the United States. Agricultural Handbook No. 450.

Vander Wall, S. B., and R. P. Balda. 1977. Coadaptations of Clark's Nutcracker and the pinyon pine for efficient seed harvest and dispersal. Ecol. Monogr. 47:89–109.

______. 1981. Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Z. Tierpsychol. 56:217–241.

Wright, R. D., and H. A. Mooney. 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains of California. Amer. Midl. Nat. 73:257–284.

INCIDENCE OF THE LEECH *HELOBDELLA STAGNALIS* ON THE COLORADO RIVER IN WEST CENTRAL COLORADO

Mitra Malek[1] and Gary McCallister[1]

Abstract.— Fifty-seven fish of three genera were taken from the Colorado River in west central Colorado and examined for external parasites. No external parasites were found on *Ictalurus*. Seven percent of the *Hybognathus* and 100 percent of the *Catastomus* were infected with a Hirudinean of the species *Helobdella stagnalis*.

The Colorado River is a major drainage of the American Southwest. One of the first large tributaries to join the Colorado is the Gunnison River, which drains the south central Colorado Rocky Mountains. These two rivers join on the southwest edge of the city of Grand Junction, Colorado, in a large valley. In this area there are a number of rapids alternating with deeper, still channels to give a variety of habitats.

Of the 44 species of freshwater leeches in the United States (Pennak 1978), only the Piscicolidae generally attack fish. They attach to fish periodically, take a blood meal, and then abandon the host for a time. Their life cycles are not well known, and fish host specificity appears to be lacking (Hoffman 1970).

Methods

In this study, 57 fish were caught by seining from the Colorado River in west central Colorado, on the outskirts of Grand Junction, Colorado. Samples were taken only during the months of April and May in 1982 and 1983, and all samples were captured close to the shore, as spring currents are treacherous. The surface of each fish was examined with a dissecting microscope at magnifications of 4X. The number of leeches on each fish were recorded and the fish host identified.

Leeches were placed in the lid of a petri dish in a small amount of water. The inverted bottom of the dish was then placed over the leech to keep it flattened. Seventy percent ethanol was gradually added until movement ceased, usually 15 to 30 minutes. Specimens were then washed in 70% overnight, then stored in vials of 80% ethanol. A few specimens were fixed in Schaudinn's fluid overnight and then washed in two changes each of 50% and 70% ethanol, for 30 minutes in each change. The specimens were stained with borac carmine overnight; then destained in 70% acid alcohol. Dehydration of the specimen was accomplished by passage through 70, 80, 90, and 100% ethanol, then cleared in xylene and mounted in permount.

Results

Fifty-seven fish belonging to three species were examined (Table 1). The smallest sample was of *Ictalurus metas*, a catfish. All specimens of this species were relatively small, averaging 4 cm in length, and none were found to have leeches attached. The largest group of fish was of the Silvery Minnow (*Hybognathus nuchalis*), of which 3 of

Table 1. The hosts, numbers collected, percent infected, and the mean number of leeches per host for fish collected from the Colorado River in west central Colorado.

Host (Genus)	Number sampled	Number infected	Percent	$\bar{x}$ Leeches/ infected host
Catostomus	11	11	100	3
Hybognathus	43	3	7	1
Ictalurus	3	0	0	0

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43 (7%) were infected. Each infected fish of this species had only one external parasite. The 11 *Catastomus latipinnis* (suckers) were all (100%) infected and averaged 3 leeches per host (varying from 1 to 8 each). All leeches on the 14 infected fish were identified as *Helobdella stagnalis*. Tentative identification was made by the authors and then confirmed by Dr. Bruce Bauerle, Biology Department, Mesa College, Grand Junction, Colorado.

DISCUSSION

The water arriving at the Colorado River from the Gunnison River tributary somewhat changes the volume and nature of the Colorado River below the confluence. The Gunnison has crossed a 40-mile stretch of exposed lowland and has warmed slightly prior to joining the Colorado River. On the days of seining, there was a 3 C difference in temperature between the two rivers. The added turbulence, volume, food supply, and temperature may create habitats that do not exist upstream in the Colorado River.

Helobdella stagnalis appears to be a cosmopolitan and common Hirudinea (Pennak 1953, Young and Ironmonger 1980). It usually makes its way in the world as a scavenger, or predator of small invertebrates such as oligochaets, chironomids, and gastropods (Young and Ironmonger 1980). It occasionally is reported on fish or amphibians, and will rarely take blood from man. Its geographic presence in Colorado is not surprising because of its cosmopolitan nature. Its uniform presence on *Catostomus* in these samples is unusual. This appears to be the first report of *Helobdella stagnalis* in the upper Colorado River drainage and also the first report of this leech on *Catostomus*.

LITERATURE CITED

HOFFMAN, G. L. 1970. Parasites of North American freshwater fishes. Univ. of California Press, Los Angeles.

PENNAK, R. W. 1953. Fresh-water invertebrates of the United States. The Ronald Press Co., New York.

YOUNG, J. O., AND J. W. IRONMONGER. 1980. A laboratory study of the food of three species of leeches occurring in British Lakes. Hydrobiologia 68(3):209–215.

FIELD ESTABLISHMENT OF FOURWING SALTBUSH IN PROCESSED OIL SHALE AND DISTURBED NATIVE SOIL AS INFLUENCED BY VESICULAR-ARBUSCULAR MYCORRHIZAE[1]

C. A. Call[2] and C. M. McKell[3]

Abstract.— Seedlings of fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) were inoculated with indigenous vesicular-arbuscular mycorrhizal (VAM) fungi in a containerized system and transplanted into processed oil shale and disturbed native soil in a semiarid rangeland environment in northwestern Colorado. After two growing seasons in the field, plants inoculated with VAM had greater aboveground biomass, cover, and height than noninoculated plants. Mycorrhizal plants were more effective in the uptake of water and phosphorus. Infection levels of inoculated plants were greatly reduced in processed shale (from 13.0 at outplanting to 3.8 at harvest), but functional VAM associations could be found after two growing seasons. Results indicate that VAM help make processed oil shale a more tractable medium for the establishment of plants representative of later successional stages by allowing these plants to make effective use of the natural resources that are limiting under conditions of high stress.

Processed oil shale is biologically sterile, highly alkaline (pH of 8 to 12), highly saline (EC_e of 6 to 26 mmhos/cm), and deficient in available nitrogen (N) and phosphorus (P) (Institute for Land Rehabilitation 1979, Schmehl and McCaslin 1973). Relatively few studies have been conducted in the United States using untreated processed shale as a plant growth medium, and the results have generally been disappointing. Schmehl and McCaslin (1973) observed that germination and seedling growth of tall wheatgrass (*Agropyron elongatum* (Host) Beauv.) and Russian wildrye (*Elymus junceus* Fisch.) were significantly lower on processed shale than on soil. Merkel (1973) reported poor establishment of 10 direct-seeded grass, forb, and shrub species and several transplanted shrub species on untreated spent shale. In a similar study (Baker and Duffield 1973), several weedy species invaded untreated spent shale plots originally seeded with several shrub and perennial grass species.

Intensive treatments (leaching salts from the root zone, fertilization, mulching, and periodic supplemental irrigation) allow a variety of plant species to be directly established on processed shale (Bloch and Kilburn 1973, Harbert and Berg 1974). However, these treatments may not be feasible on a commercial scale due to their high cost or the unavailability of resources.

McKell (1978) proposed a strategy for the rehabilitation of processed oil shale piles that would work within the environmental constraints of affected arid and semiarid ecosystems and be more cost effective than those strategies that recommend extensive modifications of the spent shale. Local ecotypes of dominant plant species would be propagated, grown in containers, and transplanted into soil trenches surrounded by surface-treated water catchment slopes. Minimal fertilization and supplemental irrigation would be used only when necessary during the initial establishment period. Indigenous vesicular-arbuscular mycorrhizae may prove to be vital to the success of this minimum-treatment rehabilitation strategy.

Vesicular-arbuscular mycorrhizae (VAM) enhance plant absorption of P and other elements, enhance water uptake and transport in plants, and allow plants to withstand high temperatures (Gerdemann 1975). Vesicular-arbuscular mycorrhizae are also key links in nutrient cycling and energy flow processes in ecosystems (Trappe and Fogel 1977).

When soils are disturbed there is a reduction in VAM fungal propagules and a lower potential for infection of new host plants

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(Miller 1979, Reeves et al. 1979). The greater the disturbance, the greater is the potential for elimination of mycorrhizal propagules and, therefore, a longer time is required for reestablishment of mycorrhizal vegetation.

The success of a minimal-treatment revegetation program for processed oil shale piles and disturbed soils may depend, in part, on developing methods to introduce VAM fungi into disturbed sites where they are absent. The inoculation of nursery bed or container media with VAM fungi, in combination with reduced fertility levels, could produce plants better adapted to the environmental conditions of the outplanting site and provide a source of inoculum for other desirable plant species that require VAM associations for successful establishment.

A field study was undertaken to determine if the inoculation of fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.) with VAM fungi would provide plants better adapted for a minimal-treatment revegetation program for processed oil shale and disturbed native soil.

Study Area

Upon initiation of this research in 1977, all field experiments were to be conducted on or adjacent to Federal Oil Shale Lease Tracts Ua and Ub in northeastern Utah. Due to the size of the study plot required, and the logistics and cost of hauling Paraho processed shale from the Anvil Points retort in northwestern Colorado to the Ua/Ub study site, field outplanting studies were moved to Anvil Points in 1979. Indigenous VAM fungal inoculum was collected on tracts Ua and Ub prior to the relocation of field outplanting studies to the Anvil Points site.

Tracts Ua and Ub are approximately 80 km southeast of Vernal, Utah, and are between 1520 and 1850 m above sea level. The climate of the area is semiarid, with annual precipitation ranging from approximately 230 to 280 mm. Shallow soils (less than 50 cm deep) on sloping to steep upland terraces are light-colored, moderately calcareous channery loams and channery sandy loams (VTN Colorado, Inc. 1977). Deep soils (greater than 150 cm deep) in drainage areas range from light-colored, moderately sandy or channery loams to strongly alkaline, highly saline, sandy loams (VTN Colorado, Inc. 1977). Sagebrush-greasewood (*Artemisia tridentata* Nutt.-*Sarcobatus vermiculatus* (Hook.) Torr.), shadscale (*Atriplex confertifolia* (Torr. and Frem) Wats.), juniper (*Juniperus osteosperma* (Torr.) Little), and riparian vegetation types are found on tracts Ua and Ub (VTN Colorado, Inc. 1977). *Atriplex canescens* is found in all four vegetation types.

The Anvil Points Oil Shale Research Facility is 11.2 km west of Rifle, Colorado, and approximately 130 km southeast of tracts Ua and Ub in Utah. In 1975, a 55 x 122 m open area was filled with Paraho processed shale (maximum particle size of 3.8 to 6.5 cm) to a depth of 2.7 m (U.S. Dept. of Interior 1976). In 1978 two 50 cm-deep, v-shaped parallel trenches were constructed across the width of the shale pile and filled with a disturbed channery loam (Soil Conservation Service 1980), obtained adjacent to the site. The study site is 1722 m above sea level. The climate of the area is semiarid, with annual precipitation averaging 305 to 357 mm (Harbert and Berg 1974). The surrounding vegetation is the low elevation pinyon-juniper (*Pinus edulis* Engelm.-*Juniperus osteosperma* (Torr.) Little) woodland type (Ward et al. 1974).

Methods

Isolation and Culture of Inoculum

During September 1977 5-kg soil samples were collected beneath three individuals of *A. canescens* on tracts Ua and Ub. Soil samples were maintained at 4 C until the time of processing a few days later. Spores of VAM fungi were collected from the soil using a wet-sieving and decanting technique (Gerdemann and Nicolson 1963), and identified according to the taxonomic interpretations of Gerdemann and Trappe (1974). The two spore types most commonly observed in the wet-sieved soil were identified as *Glomus fasciculatus* (Thaxt. sensu Gerd.) Gerdemann and Trappe, and *Glomus mossae* (Nicol. and Gerd.) Gerdemann and Trappe. Spores of *G. fasciculatus* were more abundant than spores of *G. mosseae*. Spores of both species were surface-sterilized in 0.05% sodium hypochlorite for 10 minutes and rinsed three times in distilled water prior to being introduced as a mixture into pot cultures.

Initial pot cultures were established in surface-sterilized 14 cm plastic pots in the greenhouse. Approximately 75 to 100 surface-sterilized spores were pipetted in a layer within a sand-soil medium (2:1, v/v) that had been steam sterilized for two hours on each of two consecutive days. Seeds of sudangrass (*Sorghum vulgare* Pers.) were surface sterilized for 10 minutes in 0.5% sodium hypochlorite, rinsed three times in distilled water, and then placed on the surface of inoculated pot culture medium and covered with a 2 cm layer of sterilized sand-soil medium. Pot cultures were fertilized with 250 ml per pot of water-soluble fertilizer (172 ppm N, 75 ppm P, and 160 ppm K) once every month and watered sparingly by hand. Supplemental flourescent lighting was used to extend the day length to 16 hours. After four months, aboveground portions of the host plants were removed and discarded, and the pot culture medium was mixed and used to inoculate the plant growth medium for container-grown plants.

Inoculation of Experimental Plants

Approximately 250 cc of pot culture inoculum, containing propagules (spores, infected rootlets) of *G. fasciculatus* and *G. mosseae*, were placed in two layers within container medium (peat moss–perlite–sand–soil, 1:1:2:4, v/v; steam sterilized for two hours on each of two consecutive days) in 5 × 5 × 25 cm, paraffin-coated, paperboard containers. Surface-sterilized seeds (same treatment as used for sudangrass seeds) of *A. canescens* were placed in inoculated and noninoculated containers, and after development of the first set of true leaves, seedlings were thinned to one plant per container. Noninoculated seedlings were initially watered with a leachate from the pot culture inoculum to introduce soil microorganisms other than VAM fungi. Inoculated and noninoculated *A. canescens* seedlings were then fertilized in the same manner as *S. vulgare* plants and watered sparingly by hand. Supplemental flourescent lighting was used to extend day-length to 16 hours. Plants were hardened-off over a two-week period outside the greenhouse.

Inoculated and noninoculated plants were assessed for mycorrhizal development prior to transplanting and at the termination of the experiment. Root samples were cleaned of debris, cut into 1-cm segments, cleaned in 10% KOH, and stained in .05% trypan-blue in lacto-phenol (Phillips and Hayman 1970). Stained root segments were mounted in clear lacto-phenol and examined under a compound microscope at 140X for the presence or absence of VAM infection. A root segment was considered infected if it contained arbuscules, vesicles, or peletons, or any combination of the three. Percentage infection for a plant was calculated as the number of segments with any infection out of a random sample of 100 segments.

Experimental Procedures

Inoculated and noninoculated plants, ranging in height from 15 to 17 cm, were outplanted 5 June 1979 on processed shale and disturbed soil at the Anvil Points site. The split-plot design had five plants per treatment. Screen-caged, single junction, thermocouple psycrometers (J. D. R. Merrill Specialty Equipment Co., Logan, Utah) were placed beneath each plant at a depth of 30 cm (approximately 5 cm below each soil plug) to measure soil/shale water potentials. Plants in every treatment were fertilized with 34 kg/ha N as NH_4NO_3 (granular 34-0-0) and 34 kg/ha P as $Ca(H_2PO_4)_2 \cdot H_2O$ (granular 0-46-0) and given 1 *l* of water. Plant height and soil/shale water potentials were recorded at approximately three-week intervals during the two growing seasons. A Wescor HR-33T Dew Point Microvoltmeter (Wescor, Inc., Logan, Utah) was used to measure the microvolt output of each psychrometer after a 15-second cooling period. All readings were taken at dawn.

Plant water potentials were also measured at three-week intervals during the second growing season. Salt accumulation on the external leaf surface of *A. canescens* made it impossible to accurately measure plant water potential by psychrometric techniques. Therefore, plant water potential was measured with a pressure bomb (Soil Moisture

Equip. Corp., Santa Barbara, California) using the method of Waring and Cleary (1967). Cut stem tips (about 10 cm long), from the same approximate location on each plant, were placed in a pressure bomb and pressure was applied until sap first appeared at the cut end. All readings were taken at dawn.

Survival was measured in September of the first growing season (1979) and in June and September of the second growing season (1980). Plant cover was measured with a .25 m^2 quadrat prior to excavating plants from the soil and processed shale. Following excavation, aboveground biomass was dried at 80 C for 48 hours, weighed, ground in a Thomas-Wiley mill (1 mm mesh screen), and digested according to the method of Chapman and Pratt 1961). Phosphorus content of digested biomass was determined by atomic absorption spectrophotometry (Chapman and Pratt 1961) and total N content was determined by a modified Kjeldahl method (Horowitz 1965).

Samples of Paraho processed oil shale and disturbed native soil from the Anvil Points field site were analyzed for texture, pH, electrical conductivity, phosphorus, nitrate-nitrogen, potassium, sodium, calcium, and magnesium by the Soil Analysis Laboratory at Utah State University (Table 1).

Statistical Interpretations

Analysis of variance was used to determine the statistical significance ($P < 0.05$) of data from the split-plot field experiment. The least significant difference (LSD) test was applied to field data to determine significant differences ($P < 0.05$) in aboveground biomass, plant height, plant cover, and percent P and percent N of shoot material, and significant differences in soil/shale water potentials and plant water potentials between inoculation treatments and media treatments for each sampling date. Only the main effects (inoculation method and media type) were statistically significant at an acceptable level ($P < 0.05$). As a result, the analysis of differences among inoculation treatments were summed across media treatments and vice versa.

RESULTS AND DISCUSSION

Plant Growth Responses

After two growing seasons in the field, aboveground biomass, height, and cover of plants inoculated with VAM fungi were respectively 2.5, 1.8, and 2.2 times greater than those of noninoculated controls (Table 2). Significant differences were also observed between plants growing in disturbed soil and processed shale. Aboveground biomass, height, and cover of plants growing in soil were respectively 2.2, 1.8, and 1.8 times greater than those of plants growing in processed shale (Table 2). The low production of aboveground biomass and the small increase in height of plants in processed shale can be primarily attributed to the low water-holding capability, high EC, high pH, and general nutrient deficiency of the spent shale.

The growth responses observed in this experiment were similar to those of Williams et al. (1974) and Aldon (1978), who investigated the effects of VAM on the growth of *A. canescens* in soil and coal mine spoil material in New Mexico. In field and greenhouse studies, plants inoculated with *Glomus mosseae* had greater aboveground biomass in soil (Williams et al. 1974) and greater height and cover in coal mine spoil material (Aldon 1978) than noninoculated controls.

There were no differences in survival rates between inoculated and noninoculated plants

TABLE 1. A comparison of physical and chemical properties of Paraho processed shale and native soil from the study site at Anvil Points, Colorado.

			EC_e°°	meq/*l*		ppm		
	Texture	pH°	mmhos/cm	Na†	Ca + Mg†	p‡	$NO_3$$^{\pi}$	K†
Paraho Colorado shale	Silty gravel	8.6	8.0	52.2	92.3	3.8	2.2	293
Disturbed native soil	Channery loam	7.9	6.7	67.4	26.5	3.1	8.7	80

°Based on saturated paste
°°Based on saturation extract
†Ammonium acetate extractable
‡Sodium bicarbonate extractable
$^{\pi}$Phenodisulfonic acid extractable

in both types of media. All treatments had survival rates of 100 percent due in part to the favorable field conditions. In the 25-day period following field outplanting on 5 June 1979, *A. canescens* transplants received 11.7 mm of precipitation. This precipitation, in addition to the 1 *l* of supplemental water applied at the time of outplanting, may have overshadowed the effects of VAM in reducing transplant shock.

Nutritional Status

Plants inoculated with VAM fungi had significantly higher P contents and slightly higher N contents than noninoculated controls (Table 2). Plants growing in disturbed soil had slightly higher P contents and significantly higher N contents than plants growing in processed shale (Table 2).

Soils and spoils such as those derived from shales in northeastern Utah and northwestern Colorado are usually deficient in plant-available P (Bauer et al. 1978). Increased growth associated with mycorrhizal infection in nutrient-deficient soils and spoils has been attributed to enhanced nutrient uptake, especially the uptake of P (Aldon 1978, Daft and Nicolson 1966, Gerdemann 1975). Fungal hyphae extending from mycorrhizal roots compensate for deficiencies of immobile ions such as phosphate by exploring a greater volume of soil than roots alone, and by presenting a greater surface area for phosphate uptake (Gerdemann 1975). In addition to increasing the surface area of infected roots, VAM fungi take up phosphate much more rapidly than nonmycorrhizal roots and transfer it rapidly to the host plant via the relatively large surface area of the arbuscules (Bowen et al. 1975).

Table 2. Biomass, height, cover, and P and N contents of aboveground plant material after two growing seasons in the field for inoculated and noninoculated *A. canescens* plants grown in processed shale and disturbed soil.*

	Inoculation**		Media**	
	+M‡	−M‡	Soil	Shale
Shoot biomass (g)	60.89a	24.51b	58.89e	26.59f
Height (cm)†	33.50a	18.50b	33.35e	18.65f
Cover (cm^2)	1192a	552b	1125e	620f
P (%)	0.095a	0.071b	0.089e	0.076e
N (%)	1.76a	1.71a	1.97e	1.51f

*Values are means of five replicates.

**Means in the same row followed by the same letter are not significantly different at the 0.05 level.

‡+M = inoculation with mycorrhizal fungi, and −M = no inoculation with mycorrhizal fungi.

†Values represent increases in plant height above a base height of 15 to 17 cm at time of transplanting.

The forms and amounts of N that are available on a seasonal basis to plants in arid and semiarid environments have not been satisfactorily documented (Wallace et al. 1978). Some studies indicate that NO_3 is the major form of N taken up and assimilated by several salt desert shrub species under greenhouse conditions (Institute for Land Rehabilitation 1979) and field conditions (Wallace 1978). Nitrate moves to the root by mass flow under most conditions. Where the transfer of ions is rapid as in mass flow, uptake will be limited mainly by the absorbing capacity of the root and VAM (Bowen and Smith 1981). As a result, hyphal proliferation from mycorrhizal roots may have less effect on the uptake of NO_3 than on the uptake of P.

Soil/Shale and Plant Water Relations

During the first growing season (1979) of the field experiment, soil/shale water potentials were significantly lower under mycorrhizal transplants than under nonmycorrhizal transplants from 17 July through 9 September (Fig. 1A). The lower water potentials indicate that roots from mycorrhizal transplants may have grown more actively into soil and processed shale than roots from nonmycorrhizal transplants and extracted available soil/shale moisture near the psychrometers. It is possible that the roots (and hyphae) of inoculated plants could have reached the immediate vicinity of the psychrometers (approximately 5 cm away) within a month after outplanting since roots of a closely related species, *Atriplex confertifolia*, have been reported to grow at the rate of approximately 2 to 3 mm per day during June and July in a cool desert environment (Fernandez and Caldwell 1977). Similar trends in soil/shale water potentials were noted for inoculation treatments and media treatments during the second growing season (1980) (Figs. 1A and 1B).

Soil/shale water potential data also indicated that processed shale was a more limiting growth medium than native soil in

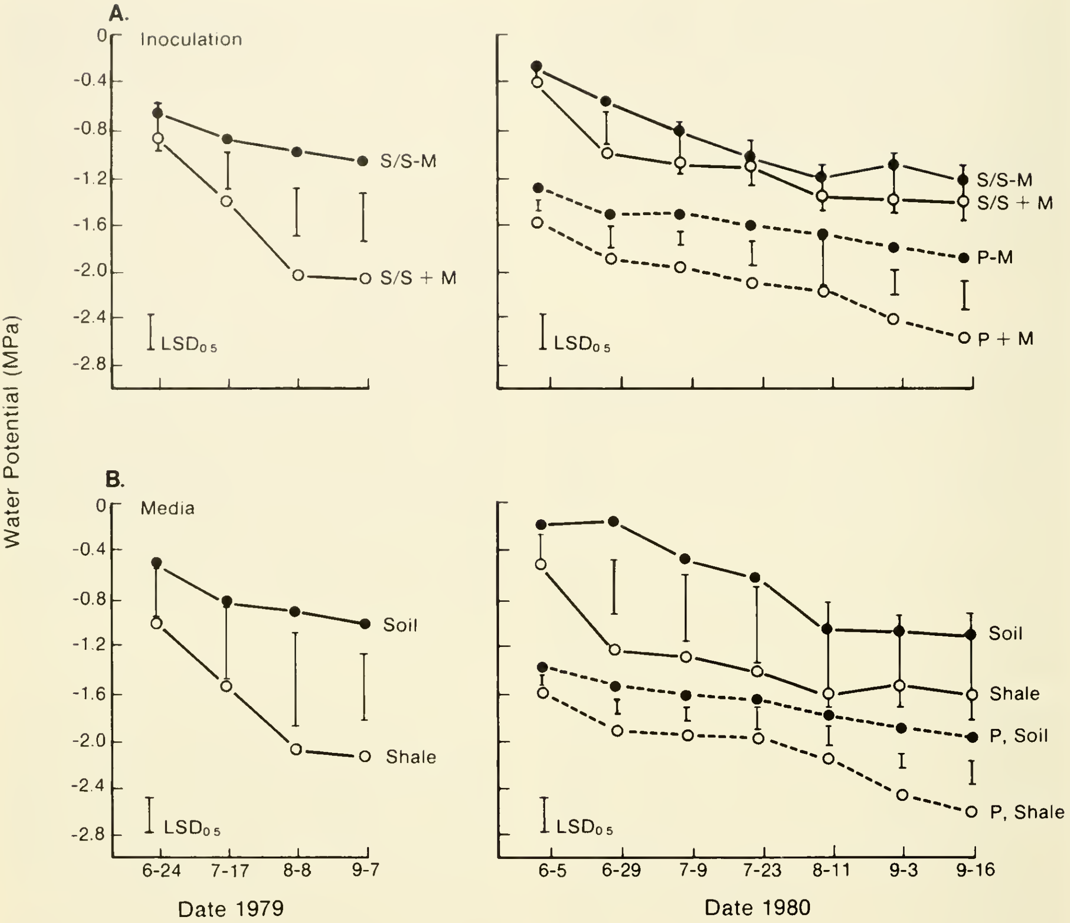

Fig. 1. Soil/shale water potentials and plant water potentials during two field-growing seasons for *A. canescens*: (A) inoculated two ways (S/S–M = soil/shale water potential under noninoculated plants, S/S+M = soil/shale water potential under inoculated plants, P–M = water potential of noninoculated plants, and P+M = water potential of inoculated plants), and (B) grown in processed shale and disturbed soil (SOIL = soil water potential under inoculated and noninoculated plants, SHALE = shale water potential under inoculated and noninoculated plants, P,SOIL = water potential of inoculated and noninoculated plants in soil, and P,SHALE = water potential of inoculated and noninoculated plants in shale).

terms of water relations (Fig. 1B). The spent shale had a higher electrical conductivity than the native soil (Table 1), and thus the osmotic potential of the shale solution was more negative than that of the soil solution. The permeability of the spent shale layer was much lower than that for the disturbed channery loam in the trench. Salts, especially Na, accumulated at the surface (EC_e of 540 mmhos/cm; McKell, unpubl. data) via capillary rise and destroyed the physical structure of the spent shale by dispersion of the fine particles (Striffler et al. 1974). The permeability of the spent shale surface was further reduced when crusting occurred as the shale dried.

Plant water potentials followed the seasonal progression of soil/shale water potentials during the second growing season (Figs. 1A and 1B). Plant water potentials were significantly lower for mycorrhizal plants than nonmycorrhizal controls for all sampling dates except 11 August (Fig. 3A). Mycorrhizal plants had greater leaf surface area for transpirational loss, and thus developed steeper gradients in water potential (from leaf to soil) than nonmycorrhizal plants. Differences in aboveground biomass may not completely account for higher transpiration rates in *A. canescens* plants inoculated with VAM fungi. In a study involving similarly sized, 8-month-old, mycorrhizal and nonmycorrhizal rough lemon (*Citrus jambhiri* Lush.) seedlings, Levy and Krikun (1980) found that mycorrhizal plants had slightly higher transpiration flux densities and stomatal conductance than nonmycorrhizal plants during a four-day period of imposed water stress and a four-day recovery period following rewatering. In that study (Levy and Krikun 1980), as in another (Allen et al. 1981) with blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.), the influence of the mycorrhizal association on plant water relations was attributed, in part, to changes in phytohormone levels.

Several investigators have studied the plant-soil water relations of *Atriplex* species in the greenhouse and in their native cool desert environments. Richardson and McKell (1980) demonstrated that *A. canescens*, growing in processed oil shale in the greenhouse, was able to adjust osmotic potentials so as to maintain positive turgor at plant water potentials exceeding -4.0 MPa. Near Federal Oil Shale Lease Tracts Ua and Ub in northeastern Utah, Barker (1978) observed measurable shoot growth for one-year-old container-grown transplants of *A. canescens* growing in soil with a water potential of -2.2 MPa at a depth of 30 cm. Love and West (1972) measured plant water potentials of up to -8.0 MPa in *A. confertifolia* in northern Utah during July and August. During July and August in the same area, other investigators working with *A. confertifolia* observed measurable root growth at -8.0 MPa soil water potential at a depth of 40 cm (Fernandez and Caldwell 1977), and positive net photosynthesis at plant water potentials exceeding -9.0 MPa (White 1976). These studies indicate that *A. canescens* plants outplanted in this study were well within their limits, and thus the effect of VAM on drought tolerance may not have been expressed fully or at all. However, VAM may have permitted greater root extension and use of available water during the establishment of these transplants.

Mycorrhizal Development

The extent of mycorrhizal infection is of importance when studying the influence of VAM on the host plant. After two growing seasons in the field, the infection percentage of inoculated plants decreased from 13.0 at outplanting to 9.8 in disturbed soil and 3.8 in processed shale. Only 0.8 percent of the root segments examined from nonmycorrhizal controls growing in disturbed soil showed evidence of infection. Nonmycorrhizal fourwing saltbush plants in processed shale showed no signs of infection. Difficulty was encountered during the excavation of roots, particularly fine root elements, from the processed shale pile and the soil trench. Fine root elements constitute the major portion of mycorrhizal roots on native shrub species (Staffeldt and Vogt 1975) and, hence, infection percentages may have been underestimated.

Water-soluble, retorted oil shale constituents probably contributed to the decline in infection of inoculated plants growing in processed shale. Hersman and Klein (1979) demonstrated that the addition of 25% processed shale to topsoil caused significant decreases in fungal populations and soil microbial activities. In another study (DeVore and Christensen 1979), root microfungi numbers were significantly reduced after in situ oil shale process water was applied to *Artemisia tridentata* plots. However, a fairly diverse microflora survived four months after the application of the process water.

Even with low infection percentages, inoculated plants still displayed positive growth responses. High infection may not be a prerequisite for growth response in all plants inoculated with VAM fungi. Abundant VAM can be present with no subsequent detectable growth difference and, conversely, a low infection level can sometimes induce marked growth stimulation (Daft and Nicolson 1966).

We conclude that VAM help make processed oil shale a more tractable medium for the establishment of plants representative of later successional stages by allowing these plants to make effective use of the natural resources that are limiting under conditions of high stress. The success of reestablishing a diverse, functional plant community that is capable of long-term stability without continued inputs of water and fertilizer may depend, in part, on success in the reinoculation and manipulation of essential microorganisms (including VAM fungi) in the initially sterile shale.

Literature Cited

Aldon, E. F. 1978. Endomycorrhizae enhance shrub growth and survival on mine spoils. Pages 174–179 *in* R. A. Wright, ed., The reclamation of disturbed arid lands. Univ. of New Mexico Press, Albuquerque.

Allen, M. F., W. K. Smith, T. S. Moore, and M. Christensen. 1981. Comparative water relations and photosynthesis of mycorrhizal and non-mycorrhizal *Bouteloua gracilis* H.B.K. Lag ex Steud. New Phytol. 88:683–693.

Baker, E. B., and W. J. Duffield. 1973. 1973 annual revegatation report. Pages 87–108 *in* M. B. Bloch and P. H. Kilburn, eds., Processed shale revegetation studies, 1965–1973. Colony Development Operation, Atlantic Richfield Company, Denver, Colorado.

Barker, J. R. 1978. The influence of containers and propagation methods on shrub growth before and after field planting. Unpublished thesis. Utah State Univ., Logan.

Bauer, A., W. A. Berg, and W. L. Gould. 1978. Correction of nutrient deficiencies and toxicities in strip-mined land in semiarid and arid regions. Pages 451–466 *in* F. W. Schaller and P. Sutton, eds., Reclamation of drastically disturbed lands. Amer. Soc. Agron., Madison, Wisconsin.

Bloch, M. B., and P. D. Kilburn. 1973. Processed shale revegetation studies, 1965–1973. Colony Development Operation, Atlantic Richfield Company, Denver, Colorado.

Bowen, G. D., D. I. Bevege, and B. Mosse. 1975. Phosphate physiology of vesicular-arbuscular mycorrhizas. Pages 241–260 *in* F. E. Sanders, B. Mosse, and P. B. Tinker, eds., Endomycorrhizas. Academic Press, New York.

Bowen, G. D., and S. E. Smith. 1981. The effects of mycorrhizas on nitrogen uptake by plants. Pages 237–247 *in* F. E. Clark and T. Rosswall, eds., Terrestrial nitrogen cycles. Ecol. Bull., Vol. 33. Swedish National Science Research Council, Stockholm.

Chapman, H. D., and P. F. Pratt. 1961. Methods of analysis for soils, plants, and waters. Univ. of California, Div. Agric. Sci., Riverside.

Daft, M. J., and T. H. Nicolson. 1966. Effect of *Endogone* mycorrhiza on plant growth. New Phytol. 65:343–350.

DeVore, B., and M. Christensen. 1979. Effect of oil shale retort effluent on soil microfungi. J. Colo. Wyo. Acad. Sci. 11(4):30.

Fernandez, O. A., and M. M. Caldwell. 1977. Root growth of *Atriplex confertifolia* under field conditions. Pages 117–122 *in* J. K. Marshall, ed., The belowground ecosystem: a synthesis of plant-associated processes. Range Sci. Dept. Sci. Ser. No. 26, Colorado State Univ., Fort Collins.

Gerdemann, J. W. 1975. Vesicular-arbuscular mycorrhizae. Pages 575–591 *in* G. Torrey, and D. T. Nicolson, eds., The development and function of roots. Academic Press, New York.

Gerdemann, J. W., and T. H. Nicolson. 1963. Spores of mycorrhizal *Endogone* species extracted from soil by wet sieving and decanting. Trans. Brit. Mycol. Soc. 46:235–244.

Gerdemann, J. W., and J. M. Trappe. 1974. The Endogonaceae in the Pacific Northwest. Mycologia Memoir No. 5, New York Botanical Garden and the Mycological Soc. of Amer., Heffernan Press, Inc., Worcester, Massachusetts.

Harbert, H. P., and W. A. Berg. 1974. Vegetative stabilization of spent oil shales. Tech. Rep. No. 4, Environ, Resources Center, Colorado State Univ., Fort Collins.

Hersman, L. E., and D. A. Klein. 1979. Retorted oil shale effects on soil microbiological characteristics. J. Environ. Qual. 8(4):520–524.

Horowitz, W. 1965. Official methods of analysis of the Association of Official Agricultural Chemists, 10th ed. Assoc. Offic. Agric. Chem., Washington, D.C.

Institute for Land Rehabilitation. 1979. Final report on revegetation studies for disturbed areas and processed shale disposal sites. Agric. Exp. Sta., Utah State Univ., Logan.

Levy, Y., and J. Krikun. 1980. Effect of vesicular-arbuscular mycorrhiza on *Citrus jambhiri* water relations. New Phytol. 85:25–31.

Love, L. D., and N. E. West. 1972. Plant moisture stress patterns in *Eurotia lanata* and *Atriplex confertifolia*. Northw. Sci. 46:44–51.

McKell, C. M. 1978. Establishment of native plants for the rehabilitation of Paraho processed oil shale in an arid environment. Pages 13–32 *in* R. A. Wright, ed., The reclamation of disturbed arid lands. Univ. of New Mexico Press, Albuquerque.

Merkel, D. L. 1973. Performance of plants with minimal treatment of processed oil shale: an interim report. Pages 75–85 *in* M. B. Bloch and P. H. Kilburn, eds., Processed shale revegetation studies, 1965–1973. Colony Development Operation, Atlantic Richfield Company, Denver, Colorado.

Miller, R. M. 1979. Some occurrences of vesicular-arbuscular mycorrhizae in natural and disturbed ecosystems of the Red Desert. Can. J. Bot. 47(6):619–623.

Phillips, J. M., and D. S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Brit. Mycol. Soc. 55:158–161.

Reeves, F. B., D. Wagner, T. Moorman, and J. Kiel. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid west. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. Amer. J. Bot. 66(1):6–13.

Richardson, S. G., and C. M. McKell. 1980. Water relations of *Atriplex canescens* as affected by the salinity and moisture percentage of processed oil shale. Agron. J. 72:946–950.

Schmehl, W. R., and B. D. McCaslin. 1973. Some properties of spent oil shale significant to plant growth. Pages 27–43 *in* R. J. Hutnik and G. Davis, eds., Ecology and reclamation of devastated land. Gordon and Breach Publ., New York. Vol. 2.

Soil Conservation Service. 1980. Written communication. Soil Conservation Service District Office, Glenwood Springs, Colorado.

Staffeldt, E. E., and K. B. Vogt. 1975. Mycorrhizae of desert plants. US/IBP Desert Biome Res. Memorandum 75-37. Utah State Univ., Logan.

Striffler, W. D., I. F. Wymore, and W. A. Berg. 1974. Characteristics of spent shale which influence water quality, sedimentation and plant growth medium. Pages 180–227 *in* C. W. Cook, coord., Surface rehabilitation of land disturbances resulting from oil shale development. Tech. Rep. No. 1, Environ. Resources Center, Colorado State Univ., Fort Collins.

Trappe, J. M., and R. D. Fogel. 1977. Ecosystematic functions of mycorrhizae. Pages 205–214 *in* J. K. Marshall, eds., The belowground ecosystem: a synthesis of plant-associated processes. Range Sci. Dept. Sci. Ser. No. 26, Colorado State Univ., Fort Collins.

U.S. Department of Interior, Bureau of Mines. 1976. Disposal of retorted oil shale from the Paraho Oil Shale Project. Final report, Denver, Colorado.

VTN Colorado, Inc. 1977. Final environmental baseline report, federal prototype oil shale leasing program tracts Ua and Ub Utah. White River Shale Project, Vernal, Utah.

Wallace, A., E. M. Romney, G. E. Kleinkopf, and S. M. Soufi. 1978. Uptake of mineral forms of nitrogen by desert plants. Pages 130–151 *in* N. E. West, and J. J. Skujins, eds., Nitrogen in desert ecosystems. Dowden, Hutchison and Ross, Inc., Stroudsburg, Pennsylvania.

Ward, R. T., W. Slauson, and R. L. Dix. 1974. The natural vegetation in the landscape of the Colorado oil shale region. Pages 33–66 *in* C. W. Cook, coord., Surface rehabilitation of land disturbances resulting from oil shale development. Tech. Rep. No. 1, Environ. Resources Center, Colorado State Univ., Fort Collins.

Waring, R. H., and B. D. Cleary. 1967. Plant moisture stress: evaluation by pressure bomb. Science 155:1248–1250.

White, R. S. 1976. Seasonal patterns of photosynthesis and respiration in *Atriplex confertifolia* and *Ceratoides lanata*. Unpublished dissertation. Utah State Univ., Logan.

Williams, S. E., A. G. Wollum, and E. F. Aldon. 1974. Growth of *Atriplex canescens* (Pursh) Nutt. improved by formation of vesicular-arbuscular mycorrhizae. Soil Sci. Soc. Amer. Proc. 38:962–965.

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NYMPHS OF NORTH AMERICAN PERLODINAE GENERA (PLECOPTERA: PERLODIDAE)[1]

Kenneth W. Stewart[2] and Bill P. Stark[3]

ABSTRACT.— Nymphs of the type or other representative species of the 22 North American Perlodinae genera are comparatively described and illustrated for the first time. The first complete generic key for the subfamily incorporates recent nymph discoveries and revisions in classification. References to all previous nymph descriptions and illustrations and major life cycle and food habits studies are given for the 53 North American species in the subfamily, and a listing of species and their current distributions by states and provinces is provided for each genus. The previously unknown nymph of *Chernokrilus misnomus* is described and illustrated.

Ricker (1952) provided the first comprehensive study of the stonefly family Perlodidae, based largely on adult genitalia and mesosternal characters, and on gills, mesosternae, and mouthparts of known nymphs. He recognized three subfamilies, Isogeninae, Isoperlinae, and Perlodinae. Stark and Szczytko (1984) discussed the subsequent disparate classifications of the family by Zwick (1973) and Ricker and Scudder (1975), and, based upon a comprehensive SEM study of eggs of world genera: (1) reaffirmed Zwick's recognition of only two subfamilies, Isoperlinae and Perlodinae, and (2) recognized three tribes of the Perlodinae, Arcynopterygini, Diploperlini, and Perlodini, containing 36 genera.

The nymphs of Perlodidae have remained relatively poorly known and/or incompletely described and illustrated, and therefore have not been comparatively studied. Ricker (1952) included notes on nymphal mouthparts, mesosternae, and gills, and a few illustrations of mouthparts (four genera), and his subsequent illustrated key to nymphs (Ricker 1959) utilized essentially those same characters. However, those papers are now incomplete since they did not include nymphs of the currently recognized genera *Calliperla* Banks, *Cascadoperla* Szczytko & Stewart, *Clioperla* Needham & Claassen, *Chernokrilus* Ricker, and *Oconoperla* Stark & Stewart. Nymphs of *Osobenus yakamae* (Hoppe) and *Rickera sorpta* (Needham & Claassen) [= *venusta* Jewett] were briefly described by Jewett (1955) and included in Ricker's (1959) key. *Calliperla* and *Chernokrilus* nymphs have remained unknown, and, at the time of the two definitive Ricker papers (1952, 1959), *Cascadoperla* (Szczytko & Stewart 1979) and *Clioperla* (Szczytko & Stewart 1981) were included in the *Isoperla*, and *Oconoperla* (Stark & Stewart 1982) had not been discovered. Szczytko and Stewart (1984b) described the nymph of *Calliperla luctuosa* (Banks), and the poorly known

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nymph of *Rickera sorpta* (Needham & Claassen). Based upon study of all life stages, they moved the genus *Rickera* from Isoperlinae to Perlodinae, and recognized seven genera in the Isoperlinae (*Bulgaroperla*, *Calliperla*, *Cascadoperla*, *Clioperla*, *Isoperla*, *Kaszabia*, and *Mesoperlina*). Shepard and Stewart (1983) described the nymphal gills of all current Perlodidae generic types except *Chernokrilus*, which is gill-less (see description below).

Our objective in this study was to provide an updated account of nymphs of the 22 North American Perlodinae genera, utilizing recent nymph discoveries and revisions in classification. The first complete generic key that follows is therefore based upon our study of known nymphs. The comparative descriptions and illustrations under each genus are based upon nymphs of the type species, except in *Cultus* Ricker and *Isogenoides* Klapálek, where good correlated nymphs of the type species were unavailable, and *Diura* Billberg and *Megarcys* Klapálek, whose types are distributed outside North America. In these four instances, common North American species whose nymphs were considered representative of the genus were used. This approach provides a complete treatment of nymphs of the 9 monospecific genera, and a useful morphological baseline for the eventual exhaustive study and analyses of nymphs of all species in the remaining 13 genera. The only comparative studies of all nymphs in a genus have been for *Diploperla* (Kondratieff et al. 1981), *Helopicus* (Stark & Ray 1983), and *Hydroperla* (Ray & Stark 1981). Accounts of each genus below also include: (1) references to all previous descriptions of North American nymphs in each genus and major life cycle and food habits studies, and (2) a list of current North American species and their known distributions by states and provinces. We began collecting and rearing nymphs of Perlodidae in 1978, giving particular attention to those that were unknown, rare, and inadequately described and illustrated. The collection of correlated nymphal study material necessary for this undertaking was successfully completed in early 1983.

MATERIALS AND METHODS

Mature nymphs of type species and others were correlated by one or more of the following methods: (1) reared in styrofoam containers in the field (Szczytko & Stewart 1979), (2) transported on ice in styrofoam containers by auto or aircraft then reared in an environmental chamber or living stream at simulated stream temperatures, or (3) heated gently in a 10% KOH solution and nymphal cuticle removed to reveal underlying adult genitalia.

Extracted mouthparts were prepared for SEM study (Stark & Stewart 1981) and photographed using an AMR 1000 scanning electron microscope at the University of Mississippi Dental School. Drawings were then made of mandibles and maxillae from the SEMs, making sure that setation and other illustrated characters could be seen with a stereo dissecting microscope. Nymphs were studied under a Wild M-5A stereomicroscope, and gills, front legs, mesosternae, abdominal venters, and cerci were drawn using a Wild Drawing Attachment. Head-pronotal patterns were prepared on stippleboard, and carbon dust habitus drawings were prepared from our pencil sketches.

Key to Subfamilies of Mature North American Perlodidae Nymphs

There are no known characters that uniformly separate nymphs of Isoperlinae from Perlodinae; however, the following key should be helpful.

1. Gills absent; lacinia bidentate (except in few eastern *Isoperla* species) and sometimes quadrate in shape; abdomen of *Calliperla*, *Cascadoperla* and most *Isoperla* with dark, longitudinal stripes .... Isoperlinae

— Combinations of submental, cervical, and thoracic gills present or absent; lacinia unidentate or bidentate and triangulate in shape; Ab without longitudinal stripes (except *Osobenus*) .... Perlodinae

Key to the 22 Genera of North American Perlodinae Nymphs

Geographic range of each genus is indicated by the following coded abbreviations (after Baumann 1976); PNA—Pan-North America (widely distributed eastern and western); ANA—Amphi-North America (distinct eastern and western populations, usually in northern latitudes); NNA—Northern North America (distributed widely across northern latitudes of the continent); WNA—Western North America (Rocky Mountains, westward); ENA—Eastern North America (Mississippi Valley, eastward); PNW—Pacific Northwest; SW—Southwest; IW—Intermountain West; NE—Northeast; SE—Southeast.

Illustrated characters referenced in the key are indicated by arrows on appropriate Figs. 1–22.

1. Gills present on 2 or more thoracic segments (Figs 12 F, E, 14 D, F) 2

— Gills absent from thoracic segments 5

2. Prothoracic gills present (Figs. 12 F, 16 F) 3

— Prothoracic gills absent (Fig. 20 F) .... *Setvena*

3. Lateral abdominal gills present on segments 1–7 (Fig. 14 D) .... *Oroperla*

— Abdominal gills absent 4

4. Anterior prothoracic gills (appearing as cervical) present, in addition to anterior supracoxal gills (Fig. 16 F) .... *Perlinodes*

— Prothorax with only anterior supracoxal gills (Fig. 12 E) .... *Megarcys*

5. Lacinia unidentate (Figs. 10 C, 18 C, 19 B) 6

— Lacinia bidentate (Fig. 1 B) 8

6. Lacinia broad basally, abruptly narrowed into a long, terminal spine (Fig. 18 C): mature nymph < 10 mm; ENA .... *Remenus*

— Lacinia gradually narrowed from base to terminal spine (Figs. 10 C, 19 B); mature nymph > 15 mm; WNA 7

7. Mesosternal furcal pits connected by transverse anterior suture (Fig. 19 E); PNW *Rickera*

— Mesosternal furcal pits without transverse anterior connecting suture (Fig. 10 E) WNA .... *Kogotus*

8. Femora and tibia with long setal fringe; (Figs. 1 D, 3 D) posterolateral margins of pronotum smoothly rounded (Fig. 1 A) 9

— Femora and tibia without long setal fringe (Fig. 13 D); posterolateral margins of pronotum notched (Fig. 13 A); SE .... *Oconoperla*

9. Mesosternum with median longitudinal suture connecting fork of Y-arms with a transverse suture (Fig. 9 F) .... *Isogenoides*

— Mesosternum without such median longitudinal suture 10

10. Occiput and/or anterolateral prothoracic margins with row of short, stout setae (Figs. 1 A, 2 A) 11

— Occiput and/or anterolateral prothoracic margins without row of short, stout setae; a few long setae may be present (Figs. 3 A, 15 A) 20

11. Mesosternal Y-arms meet or approach anterior corners of furcal pits (Figs. 1 F, 6 F, 21 F); mandibles deeply cleft (Figs. 1 C, 6 B) 12

— Mesosternal Y-arms meet or approach posterior corners of furcal pits (Figs. 2 E, 11 F, 17 F); mandibles not deeply cleft (Figs. 2 B, 11 B, 17 B) 14

12. Apical lacinial tooth short, much less than ⅓ total outer lacinial length (Fig. 6 C); ventral submarginal lacinial setae extending well onto apical tooth as a close-set row (Fig. 6 C); WNA .... *Frisonia*

— Apical lacinial tooth long, greater than ⅓ total outer lacinial length (Figs. 1 B, 21 C); ventral submarginal lacinial setae end at inner base of apical tooth (Figs. 1 B, 21 C) 13

13. Inner cusps of left mandible unserrated (outermost cusp with indistinct inner serrations) (Fig. 1 C) and serrations usually indiscernible on all cusps of right mandible; occipital area of head with sinuate spinule row, but no mesal, long, white, silky hairs; NNA .... *Arcynopteryx*

— Some inner cusps of left mandible with shallow, indistinct serrations (Fig. 21 B) and inner serrations distinct on outermost cusp of both mandibles; mesal tufts of long, white, silky hairs usually present between occipital spinule row and ecdysial suture (Fig. 21 A); WNA .... *Skwala*

14. Apical lacinial tooth about ½ total outer lacinial length (Figs. 15 C, 17 C) 15

— Apical lacinial tooth about ⅓ or less total outer lacinial length (Figs. 8 C, 11 C) 16

15. Subapical lacinial tooth ½ or less the length of apical tooth (Fig. 2 C); incomplete anterior extensions of mesosternal Y-arms present (Fig. 2 E); cerci unicolorous; PNW .... *Chernokrilus*

— Subapical lacinial tooth greater than ½ length of apical tooth (Fig. 17 C); incomplete anterior extensions of mesosternal Y-arms absent (Fig. 17 F), basal cercal segments yellow, apical ½ of cerci dark brown to black; WNA .... *Pictetiella*

16. Ventral lacinial surface with basal outer patch of more than 50 setae (Fig. 11 C); abdominal tergae generally with less than 10 short, stout intercalary setae; ENA .... *Malirekus*

— Ventral lacinial surface without basal outer patch of setae (Figs. 5 C, 7 C) or with fewer than 25 setae (Figs. 8 C, 22 C); abdominal tergae with more than 50 short stout, intercalary setae 17

17. Submental gills conspicuous, projecting portion usually 2X or more as long as their basal diameter (Figs. 7 E, 8 E) 18

— Submental gills absent or barely visible, with projecting portion no longer than basal diameter (posterolateral lobe of submentum sometimes resembles a gill) 19

18. Transverse dark pigment band of frons interrupted lateral to median ocellus by circular yellow areas (Fig. 8 A); ventral lacinial surface with outer patch of approximately 10 setae (Fig. 8 C); right mandible with 4 teeth; ENA .... *Hydroperla*

— Transverse dark pigment band of frons uninterrupted by enclosed yellow areas (Fig. 7 A); ventral lacinial surface without outer patch of setae (Fig. 7 C); right mandible with 5 teeth; ENA .... *Helopicus*

19. Marginal lacinial setal row extending from near subapical tooth to near base (Fig. 22 C); labrum with yellow longitudinal mesal band; submental gills very short if present; ENA .... *Yugus*

— Marginal lacinial setal row restricted to apical half (Fig. 5 C); labrum without longitudinal band; submental gills absent; ANA .... *Diura*

20. Abdomen with 2 broad dark longitudinal bands (Fig. 15 K); Y-arms of mesosternum meet anterior corners of furcal pits (Fig. 15 E); PNW .... *Osobenus*

— Abdomen without longitudinal dark bands; Y-arms of mesosternum meet posterior corners of furcal pits or poorly developed (Figs. 3 E, 4 E) 21

21. Mesosternal Y with basal stem and fork (Fig. 3 E) .... *Cultus*

— Mesosternal Y without stem and fork (Fig. 4 E); ENA .... *Diploperla*

Arcynopteryx Klapálek, s.s.

TYPE SPECIES.— *Arcynopteryx compacta* (McLachlan).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— (*A. compacta*) (Brink (1949; mandibles, labium/hypopharynx, labrum, maxilla, hind tarsus), Brink (1952; habitus, mandibles, labrum/hypopharynx, labrum, maxilla, hind tarsus), Despax (1951; ♂ habitus, labrum, mandibles, maxillae, labium, ♂ abdomen), Illies (1955; habitus, maxillae, ♂ abdomen), Ricker (1952; mesosternal Y-pattern) Shepard and Stewart (1983; gills).

NYMPH DESCRIPTION.— (*A. compacta*) (Figs. 1 A–K). Body brown with dark brown markings; legs, antennae and cerci light brown. Head with light M-pattern forward of anterior ocellus, light median longitudinal bar, 2 pairs light spots inside eye and sinuate occipital row of short, stout spinules (Fig. 1 A). Antennal segments with apical circlets of very short white hairs. Laciniae triangular, with 2 terminal teeth and full row of marginal and submarginal setae; terminal tooth about 0.4 total outer length of lacinia; single axillary seta (Fig. 1 B). Left mandible deeply cleft, with acanthae at base of dorsal teeth, and median ventral patch of 12–16 setae; major ventral cusp with slight serrations, inner ventral cusps without serrations (Fig. 1 C). Length of projecting portion of submental gills about 3 times their basal diameter (Fig. 1 E). Pronotum with light lateral and mesal bands and bordered with even fringe of short spinules (Fig. 1 A). Y-arms of mesosternum reach anterior corners of furcal pits (Fig. 1 F). Wingpads with numerous irregular patches of short, stout spinules. Femora and tibiae with stout spinules, clothing hairs and fine silky posterior hair fringe (Fig. 1 D). Dorsal abdominal segments with posterior fringe of short spinules and dense short, stout intercalary spinules. Male 8th abdominal sternum with 6 mesoposterior spinules (Fig. 1 G); ♀ 8th sternum with interrupted row of mesoposterior spinules (Fig. 1 H). Cercal segments with posterior whorl of spinules, dorsal intercalary spinules, and dorsal fringe of silky hairs (Fig. 1 I, J, K).

NYMPH BIOLOGY.— Relatively poorly known. Nymphs are carnivorous, feeding heavily on chironomid larvae (Brinck 1949). They inhabit cold streams and rivers (Brinck 1949) and high mountain or northern-latitude lakes with stony shoreline substrata (Baumann et al. 1977, Donald and Anderson 1980, K. W. Stewart unpubl. Alaska data).

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— *Arcynopteryx compacta* — ALAS, ALB, BC, COL, MAINE, MONT, WYO, NH, NY, SASK.

Chernokrilus Ricker

TYPE SPECIES.— *Chernokrilus misnomus* (Claassen).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— None for any species.

NYMPH DESCRIPTION.— (*C. misnomus*) (Figs. 2 A–J). Body brown with dark brown markings, covered with flat, dark clothing hairs; legs, antennae, and cerci light brown. Head with light M-pattern forward of anterior ocellus, distinct light, T-shaped marking on anterior frons, oval spots inside eyes and back of head broken by reticulate dark lines; sinuate band of stout light occipital spinules 1–3 spinules wide (Figs. 2 A, K). Antennal segments with apical circlets of short hairs. Laciniae triangular, bidentate, with 3 or 4 marginal setae below subapical tooth and along base; marginal setae absent along middle; sparse patches of submarginal setae adjacent to marginal setae; terminal tooth about 0.45 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Fig. 2 C) 2 or 3 long ventral setae on subapical tooth; single axillary seta. Left mandible without deep cleft, serrations of teeth or patch of median ventral setae; row of acanthae along base of dorsal teeth (Fig. 2 B). Gills absent. Pronotum dark brown with lateral light marginal band and reticulate markings; margined with short spinules (Figs. 2 A, K). Y-arms of mesosternum meet posterior corners of furcal pits and usually have anterior extensions not reaching anterior corners of furcal pits (Fig. 2 E). Meso-metanota dark with light reticulate markings and light wingpads (Fig. 2 K). Femora and tibiae with short, stout spinules, flat, dark clothing hairs and white, silky hair fringe (Fig. 3 D). Abdominal segments brown; terga with pairs of mesal and lateral light spots, posterior setal fringe and numerous short, stout intercalary

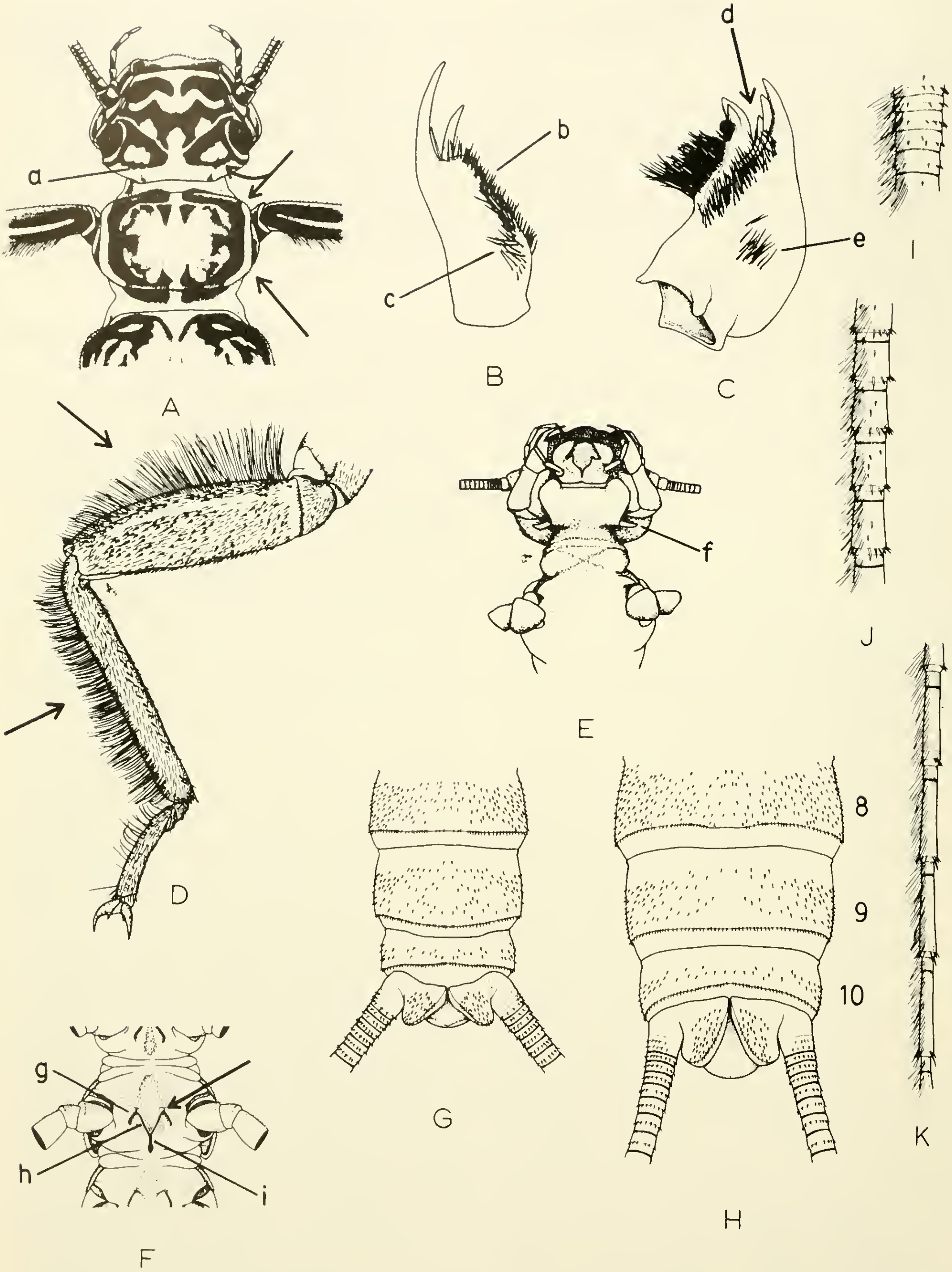

Fig. 1. Nymphal characters of *Arcynopteryx compacta*: A, head, pronotum pattern; B, right lacinia (ventral); C, left mandible (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and terminal cercal segments (dorsal); a, occipital spinule row, b, marginal lacinial setae, c, submarginal lacinial setae, d, cleft of mandible, e, median ventral setal patch of mandible, f, submental gills, g, furcal pits, h, Y-arms, i, stem of Y.

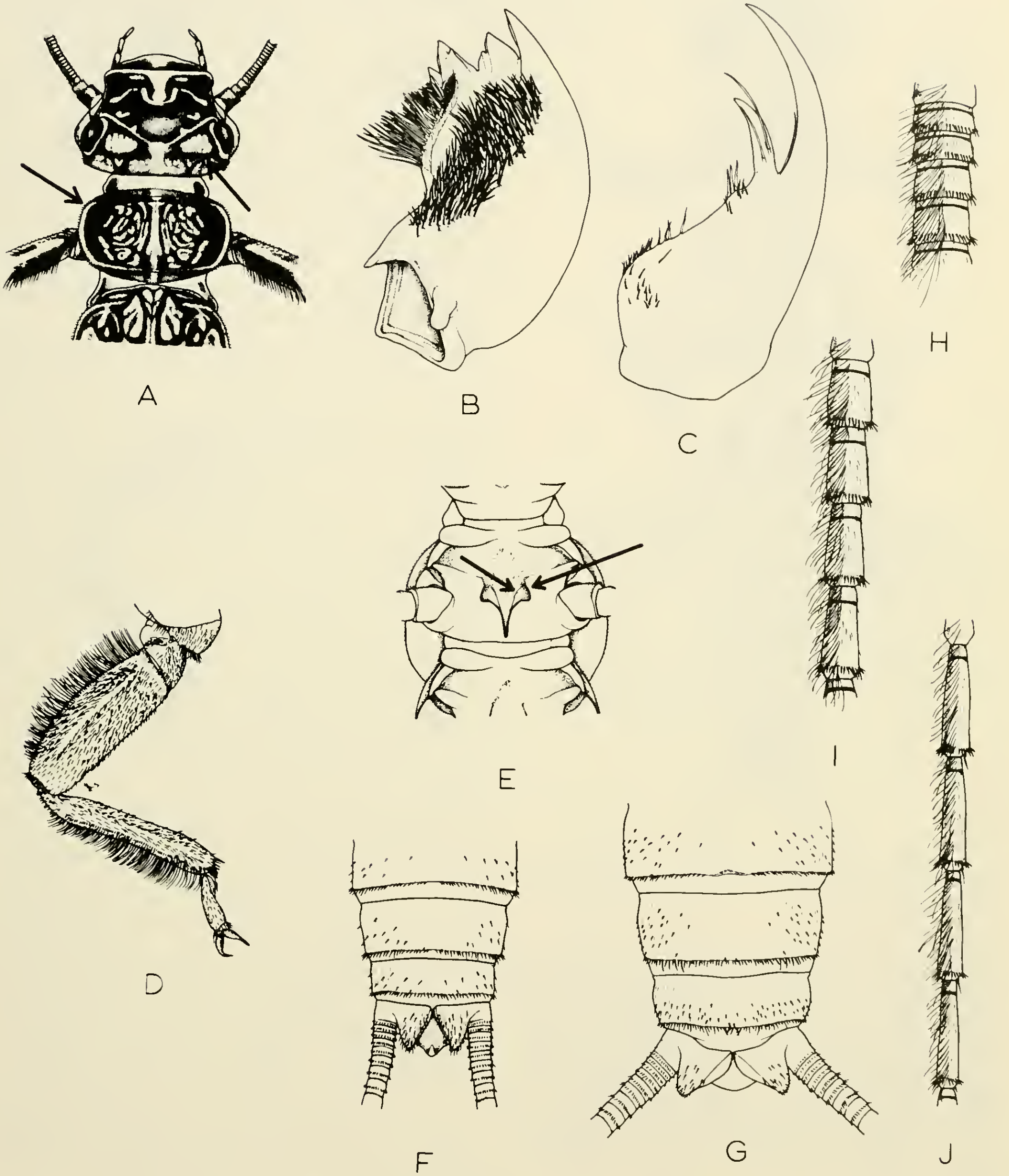

Fig. 2. Nymphal characters of *Chernokrilus misnomus*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

spinules (Fig. 2 K). Male 8th abdominal sternum with narrow mesal gap in posterior setal row (Fig. 2 F); ♀ 8th sternum with wide mesal gap in posterior setal row (Fig. 2 G). Cercal segments with dark anterior circular band, posterior whorl of setae; cerci with complete vertical fringe of silky, white hairs (Figs. 2 H–J).

NYMPH BIOLOGY.— Previously unreported for any species. We collected mature, pre-emergent *C. misnomus* nymphs in early to late May in 1982 and 1983, from headwaters

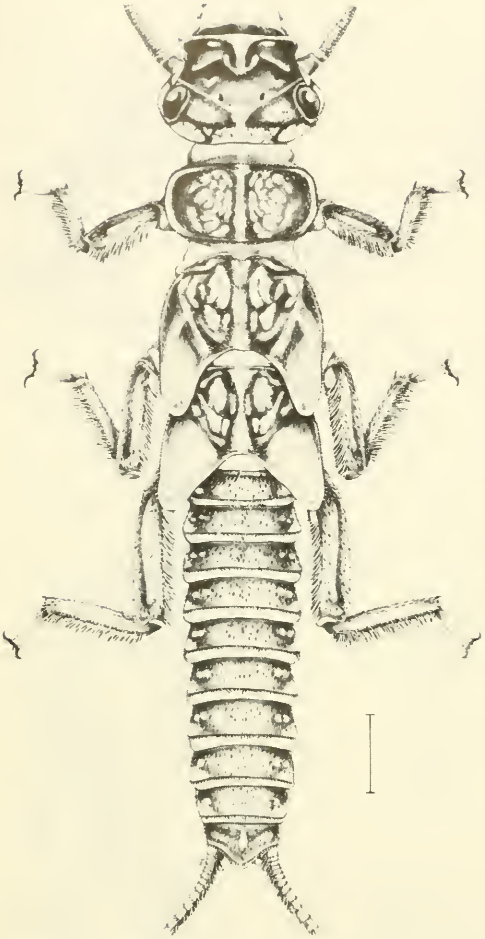

Fig. 2K. *Chernokrilus misnomus*: nymph habitus; scale line = 2 mm.

of Parker Creek, Benton County, and small steep trickles entering tributaries of the Little Nestucca River Drainage, Tillamook County, in the Coastal Range of Oregon, and in Big Spring, Siskiyou Co., California, at Mt. Shasta (7 C). Nymphs collected in Oregon after 13 May in both years were successfully field reared in styrofoam chests within 3 days.

North American species list/distribution.— (1) *Chernokrilus erratus* (Claassen) — CA, (2) *C. misnomus* — ORE, CAL, (3) *C. venustus* (Jewett) — CAL.

Cultus Ricker

Type species.— *Cultus pilatus* (Frison)

Previous nymph descriptions/illustrations.— (1) *C. aestivalis* — Baumann et al. (1977; maxilla), Ricker (1943) (as *Diploperla fraseri*), Claassen (1931) (as *Perla aestivalis*), (2) *C. decisus* — Claassen (1931; habitus, labrum, labium, mandible, maxillae), (3) *C. pilatus* — Frison (1942; habitus, mandibles, maxilla, labium), (4) *C. tostonus* —none.

Nymph description.— (*C. aestivalis*) (Figs. 3 A–J). Body yellow with brown markings; antennae, legs yellow, cerci brown. Head with variable pattern, usually with X-shaped pattern connecting ocelli, and light area anterior to median ocellus; light M pattern as in most Perlodinae usually indistinct; no occipital spinule row, but with long postorbital setae (Fig. 3 A). Antennal segments with apical circlets of short setae. Laciniae triangular, bidentate, with marginal setae restricted to tuft of 3 or 4 below base of subapical tooth; 3–4 scattered submarginal setae and patch of 12–14 submarginal setae near base; 2 or 3 axillary setae; terminal tooth about 0.4 total outer lacinial length, and subapical tooth 0.5 length of terminal tooth (Fig. 3 C). Left mandible without deep cleft, serrations of teeth or patch of median ventral setae; row of acanthae along inner base of dorsal teeth (Fig. 2 B). Gills absent. Pronotum with faint, irregular pattern; only 2 or 3 long hairs on corners (Fig. 2 A). Y-arms of mesosternum reach posterior corners of furcal pits, no transverse suture connecting furcal pits (Fig. 3 E). Wingpads with few setae on anterolateral corners and tips (Fig. 3 A). Femora and tibiae with scattered stout hairs; femora, tibiae, and tarsus with dense fringe, silky, white hairs (Fig. 3 D). Abdominal terga ringed anteriorly with brown band; posterior half yellow; no intercalary spinules; apical ring of setae with 2–5 longer mesal setae. Both ♂ and ♀ 8th abdominal sternae with mesoposterior interruption of posterior spinules (Fig. 3 F, G). Cercal segments with posterior whorl of short setae and complete dorsal fringe of silky, white hairs (Figs. 3 H, J).

Nymph biology.— Relatively poorly known for the genus. Nymphs of *C. aestivalis* inhabit a wide variety of creeks and rivers from 6950 to 9025 ft elevation in central Colorado (Knight 1965). Emergence is spread over a long period from Apr. to Aug. in the Rocky Mts. (Baumann et al. 1977, Gaufin et al. 1972); therefore, mature nymphs should be found throughout summer at various ele-

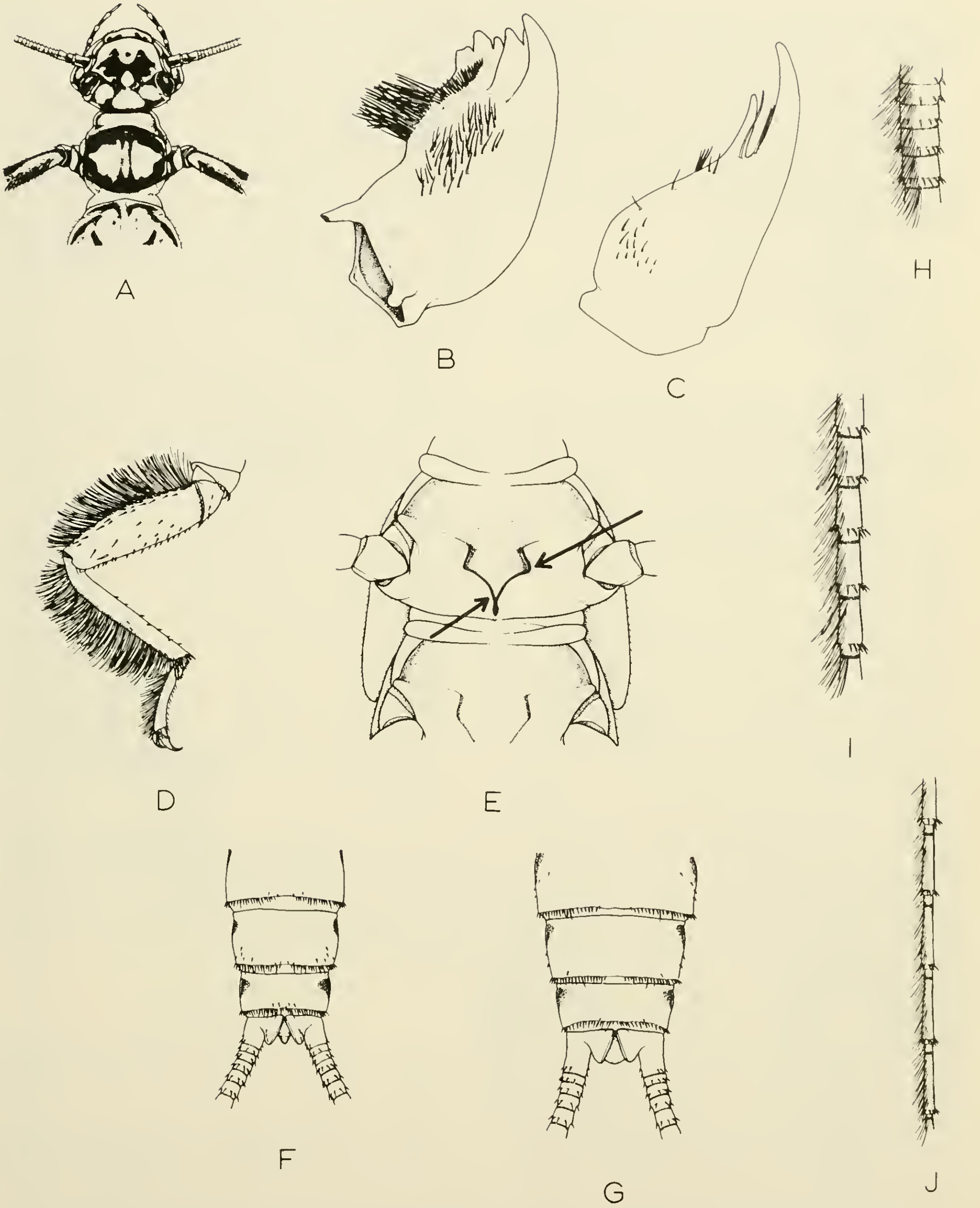

Fig. 3. Nymphal characters of *Cultus aestivalis*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

vations. Eighty-two late instar nymphs from the Dolores and Gunnison rivers, Colorado, fed almost exclusively on Chironomidae and other Diptera larvae, primarily simuliids (Fuller and Stewart 1977, 1979). Nymphs of *C. decisus* live in riffles in leaf packs and beneath stones, exhibit a univoltine cycle with most rapid nymphal growth from Feb. to emergence in Apr.–May, and are carnivorous (Minshall and Minshall 1966).

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— (1) *Cultus aestivalis* (Needham & Claassen) – ARIZ, BC, COL, ID, MONT, NM, UT, WYO, YUK, (2) *C. decisus* (Walker) – CONN, GA, IND, KY, MAINE, NC, NY, ONT, PA, QUE, TN, VA, WV, (3) *C. pilatus* (Frison) – BC, CAL, ID, MONT, ORE, WN, (4) *C. tostonus* (Ricker) – BC, CAL, ID, MONT, ORE, WN, WYO.

Diploperla Needham & Claassen

TYPE SPECIES.— *Diploperla duplicata* (Banks)

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— (1) *D. duplicata* – Hitchcock (1974; habitus), Kondratieff et al. (1981; habitus), (2) *D. morgani* – Kondratieff et al. (1981; habitus), (3) *D. robusta* – Frison (1935, labrum, mandible, maxilla, labium, habitus), Stark and Gaufin (1974), Kondratieff et al. (1981; habitus).

NYMPH DESCRIPTION.— (*D. duplicata*) (Figs. 4 A–G). Body yellow with brown markings; legs yellow, antennae and cerci brown; tiny dark, flat clothing hairs on dorsum of head, thorax. Head with brown, dark M-band connecting ocelli, with narrow light M forward of it; no distinct row or band of occipital spinules (Fig. 4 A). Laciniae triangular, bidentate with no marginal setae and only 4–6 submarginal setae; single axillary seta at base of both teeth; terminal tooth about 0.5 total outer lacinial length and subapical tooth about 0.6 length of terminal tooth (Fig. 4 C). Left mandible without deep cleft, distinct serrations of teeth (SEM 1000X shows only shallow crenulations) or patch of median ventral setae; distinct acanthae absent from base of dorsal teeth (Fig. 4 B). Gills absent. Pronotum with light, narrow lateral margins and 2 lateral longitudinal dark bands broken by reticulate light markings; narrow dark mesal line; 3–5 long setae on corners, absent laterally (Fig. 4 A). Y-arms of mesosternum incomplete, fork and stem absent, arms reaching posterior corners of furcal pits (Fig. 4 E). Meso-metanota with few short setae on anterior corners and inner margins of wingpads; irregular reticulate pattern. Femora with numerous long, stout dorsal setae; no silky hair fringe (Fig. 4 D). Tibiae with short, stout setae and golden, silky hair fringe, and tarsus with golden dorsal hair fringe (Fig. 4 D). Abdominal terga uniform brown with apical whorl of setae; 2–4 posterolateral setae on each side of each abdominal tergum as long as succeeding segments; dorsal intercalary spinules, if present, fewer than 8 and indistinct. Cercal segments with whorl of long hairs, some as long as succeeding segment; no silky dorsal fringe (Fig. 4 F). Posterior setal row of 8th abdominal sternum of both male and female interrupted; mature female nymph with shallow mesoposterior notch (Figs. 4 G, H).

NYMPH BIOLOGY.— Relatively poorly known except for *D. robusta*. Nymphs of *D. duplicata* occupy leaf or detritus packs in small Appalachian streams, have a one-year life cycle with emergence in spring, and are carnivorous (Frison 1935). They are found above 1000 ft elevation in northwestern South Carolina (McCaskill and Prins 1968). *D. robusta* emerge in May in West Virginia, nymphs were absent May–Jul. when eggs were possibly diapausing, and young nymphs appeared in Aug., grew steadily during winter and at a rapid rate in Mar.–Apr. prior to emergence, and fed primarily on chironomids, other diptera, and mayflies, Ashley et al. (1976).

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— (1) *Diploperla duplicata* – ALA, DEL, GA, MISS, SC, IN, VA, WV, (2) *D. morgani* Kondratieff & Voshell – VA, WV, (3) *D. robusta* Stark & Gaufin – CONN, IND, KY, OH, PA, VA, WV.

Diura Billberg

TYPE SPECIES.— *Diura bicaudata* (Linnaeus).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— (1) *D. bicaudata* – Nymphs from Europe have been described and illustrated by Hynes (1941, 1958), Brinck (1952), and Illies (1955), and a brief description of a single female nymph from Saskatchewan was given by Dosdall and Lemkuhl (1979), (2) *D. knowltoni* – Frison (1937), Frison (1942; mandible, maxilla, labium, habitus), Baumann et al. (1977; maxilla), (3) *D. nanseni* – Nymphs from Europe have been described and illustrated by Brinck (1949, 1952) and Saltveit (1978).

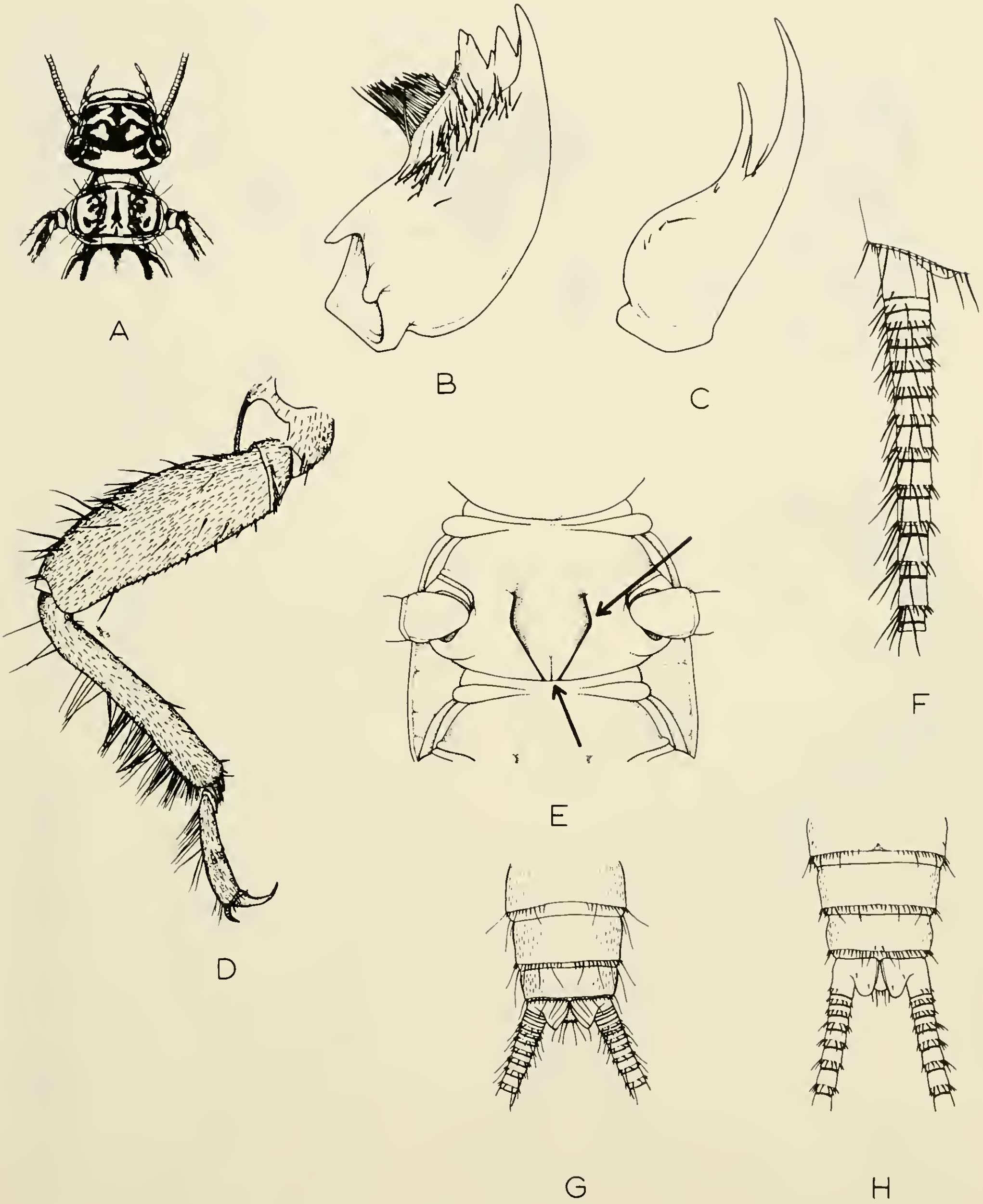

Fig. 4. Nymphal characters of *Diploperla duplicata*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, basal segments of left cercus (dorsal); G, ♂ ventral abdomen; H, ♀ ventral abdomen.

NYMPH DESCRIPTION.— (*D. knowltoni*) (Figs. 5 A–J) Body yellow to light brown with brown markings; antennae and legs light brown, cerci brown. Head with X-shaped pattern connecting ocelli, forward of which is an inverted bell-shaped light pattern; 2 light round spots inside eyes and mesal light bell-shaped mark from between lateral ocelli to occiput; postocular spinules and sparse sinuate row of indistinct occipital spinules present (Fig. 5 A). Laciniae triangular, bidentate with inner marginal setae only along apical

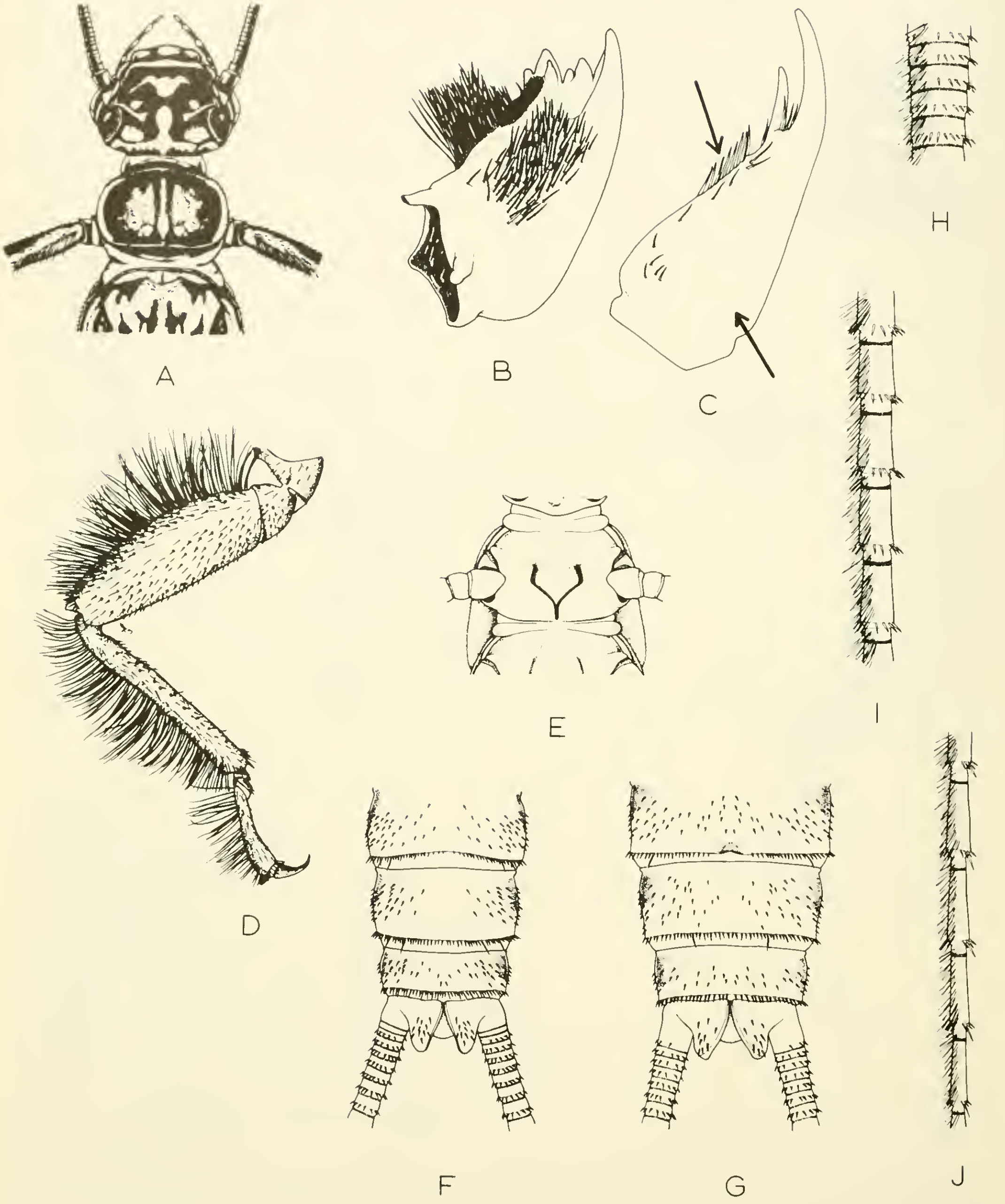

Fig. 5. Nymphal characters of *Diura knowltoni*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

half; full row of about 10 submarginal setae and 2 or 3 axillary setae; terminal tooth about 0.3 total outer lacinial length, and subapical tooth 0.5 length of terminal tooth (Fig. 5 C). Left mandible without deep cleft, serrations of teeth or patch of median ventral setae; row of acanthae along inner base of dorsal teeth. Gills absent. Pronotum with light, narrow lateral margins and mesal stripe; with submarginal brown band and interior reticulate dark lines on a light background; short spinules on anterior, posterior margins, few or none laterally (Fig. 5 A). Wingpads with mesal mushroom-shaped light pattern and short, stout setae laterally (Fig. 5 A). Y-arms of mesosternum reach posterior corners of furcal pits (Fig. 5 E). Femora with short setae, a longitudinal dark marking apically and fringe of golden, silky hairs (Fig. 5 D). Tibiae and tarsi with golden, silky hair fringe (Fig. 5 D). Abdominal terga brown with pair of large, light mesal spots giving overall appearance of a wide, central, light longitudinal abdominal band; each segment with apical setal row and more than 50 sharp intercalary spinules. Cercal segments with whorl of short setae less than 0.5 length of segments; complete dorsal fringe of short, golden, silky hairs (Fig. 5 H–J). Posterior setal row of male 8th abdominal sternum little interrupted (Fig. 5 F); a wide mesal interruption of setae, and a shallow notch on female 8th abdominal sternum (Fig. 5 G).

NYMPH BIOLOGY.— Relatively poorly known for the North American *D. knowltoni*. It is found in small streams and larger rivers with stony substrata at 7,220–10,300 ft elevation in Gunnison River drainage, Colorado (Knight 1965, Knight and Gaufin 1966). Emergence is in Apr.–Jun. in Pacific Northwest and Rocky Mountains (Jewett 1959, Baumann et al. 1977). Sheldon (1972) found *D. knowltoni* only above 1810 m in Sagehen Crk and above 1900 m in the Little Truckee River. Nymphs were strict carnivores, with major prey items split between Diptera and Trichoptera larvae. Small nymphs were first collected in Aug. and growth was continuous through fall and winter until emergence in May and Jun. There are no reports on the biology of *D. bicaudata* and *D. nanseni* nymphs in North America. Both species have univoltive cycles in Sweden, with rapid growth in autumn (Aug.–Oct.) and spring (Apr.–Jun.), slowed growth in winter (Oct.–Mar.), and emergence in Jun.–Jul., and both are carnivorous, feeding primarily on mayfly nymphs and diptera larvae (Brinck 1949).

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— (1) *Diura bicaudata* — ALAS, NWT, YUK, (2) *Diura knowltoni* (Frison) — ALB, BC, COL, ID, MONT, NEV, NM, OR, SASK, UT, WYO, YUK, (3) *D. nanseni* (Kempny) — NH, QUE.

Frisonia Ricker

TYPE SPECIES.— *Frisonia picticeps* (Hanson).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— Ricker (1943; mandible, maxilla), Ricker (1959, written description in key for subgenus *Frisonia* was erroneously given under subgenus *Skwala*).

NYMPH DESCRIPTION.— (Figs. 6 A–L) Body brown with dark brown markings; legs light brown, antennae and cerci brown. Dark clothing hairs lying flat over whole dorsal surface and legs. Head mostly brown with faint M-pattern anterior to median ocellus and 2 light spots posterior to M (Fig. 6 A, L); sinuate row of occipital spinules, interrupted mesally. Bushy band of long, white shaggy hairs across back of head between eyes, and mesally from prothorax to tip of abdomen (Fig. 6 L). Laciniae triangular, bidentate, and strongly curved, with full row of very stout marginal and submarginal setae and 3 axillary setae; row of 10–12 stout setae extending up onto ventral basal portion of terminal tooth; terminal tooth about 0.3 total outer lacinial length and subapical tooth about 0.6 length of terminal tooth (Fig. 6 C). Left mandible deeply cleft with prominent serrations of teeth; without median ventral setal patch; row of acanthae along base of dorsal tooth (Fig. 6 B). Submental gills prominent, about 2 times their basal diameter (Fig. 6 E). Pronotum brown with light mesal longitudinal band, light reticulate markings and short marginal spinules (Fig. 6 A). Wingpads with reticulate pattern and short marginal spinules (Fig. 6 A). Y-arms of meso-sternum reach or nearly reach anterior corners of furcal pits (Fig. 6 F). Femora with spinules or stout setae restricted to narrow band adjacent to dorsal fringe; dense fringe of long, silky, white hairs (Fig. 6 D). Tibiae with few scattered spinules and dense fringe of long silky hairs, and tarsi with row of silky hairs (Fig. 6 D). Abdominal segments dark brown with short apical setal row and few scattered, very short, blunt intercalary spinules (Fig. 6 L).

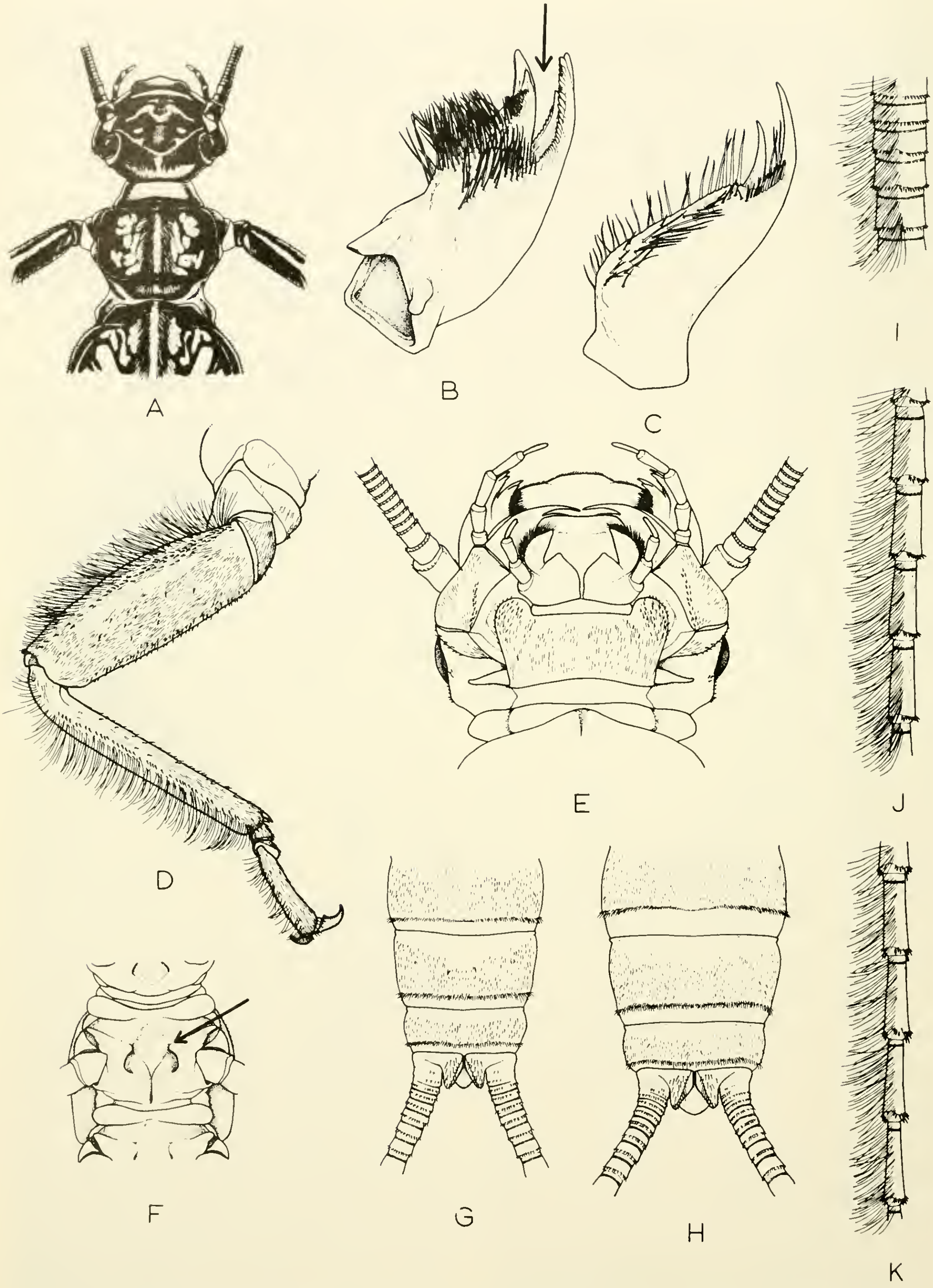

Fig. 6. Nymphal characters of *Frisonia pictipes*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

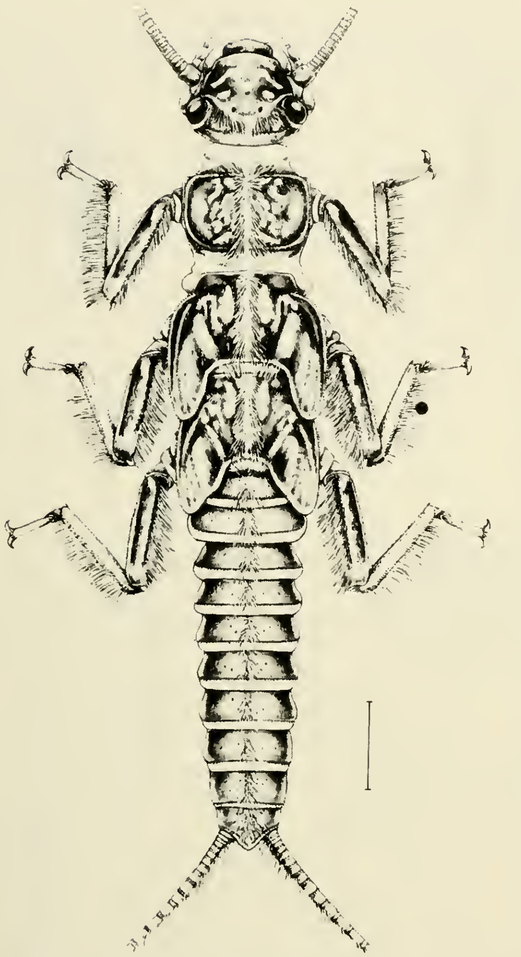

Fig. 6L. *Frisonia pictipes*: nymph habitus; scale line = 2 mm.

Cercal segments with whorl of short apical spinules, and cerci with full dorsal fringe of silky, white hairs (Figs. 6 I–K). Posterior setal row of male and female 8th abdominal segments interrupted (Figs. 6 G–H).

Nymph biology.— Relatively poorly known. Sheldon (1972) found *F. picticeps* to be relatively common in riffle samples taken above 1810 m in Sagehen Creek. Small nymphs were collected in Aug. and a continuous growth pattern was exhibited until emergence in May and Jun. Nymphs fed primarily on Diptera larvae, but considerable plant material was ingested by nymphs feeding on smaller larvae.

North American species list/distribution.— Monospecific genus; *F. picticeps* — BC, CAL, NEV, ORE, WN.

Helopicus Ricker

Type species.— *Helopicus nalatus* (Frison).

Previous nymph descriptions/illustrations.— (1) *H. bogaloosa* — Stark and Ray (1983; head/pronotum, lacinia, mandibles with acanthae, detail of occiput) (2) *H. nalatus* — Frison (1942; habitus, mandibles, labium, maxilla), Ricker (1952), Stark and Ray (1983; head/pronotum, lacinia, mandibles, labrum), (3) *H. subvarians* — Ricker (1952; habitus, maxilla).

Nymph description.— (*H. nalatus*) (Figs. 7 A–K). Body and legs yellow with brown markings; antennae and cerci yellow. Head with transverse brown band between antennae, enclosing anterior ocellus; brown spot between lateral ocelli, and irregular narrow brown bands behind arms of ecdysial suture; complete, sinuate band of stout occipital spinules 2–3 wide (Fig. 7 A). Laciniae triangular, bidentate, with row of 20–22 marginal setae, 8–10 submarginal setae, and 3 or 4 axillary setae; terminal tooth about 0.35 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Fig. 7 C). Right mandible without deep cleft, and with serrations on ventral 2 teeth; no distinctly separated median ventral setal patch; band of acanthae from base of tooth 3 to marginal setae (Fig. 7 B). Prominent submental gills, projecting portion about 3 times basal diameter (Fig. 7 E). Pronotum yellow with marginal brown band, narrow, dark mesal longitudinal band and irregular lateral, dark reticulate markings; complete marginal row of short spinules (Fig. 7 A). Y-arms of mesosternum meet posterior corners of furcal pits (Fig. 7 F). Wingpads with irregular reticulate brown markings; spinules on all margins (Fig. 7 A). Femora with posterodorsal, longitudinal brown band, apical transverse brown band, numerous stout dorsal spinules, and dense fringe of silky, yellow hairs (Fig. 7 D); tibiae with spinules, and tibiae and tarsi with dorsal fringe of silky, yellow hairs (Fig. 7 D). Abdominal terga 1–9 with anterior transverse brown band and thin brown apical margin; segment 10 with median transverse band; numerous stout intercalary spinules (> 100) and posterior fringe of setae. Cercal segments with apical whorl of short setae and complete dorsal fringe of silky, yellow hairs (Figs.

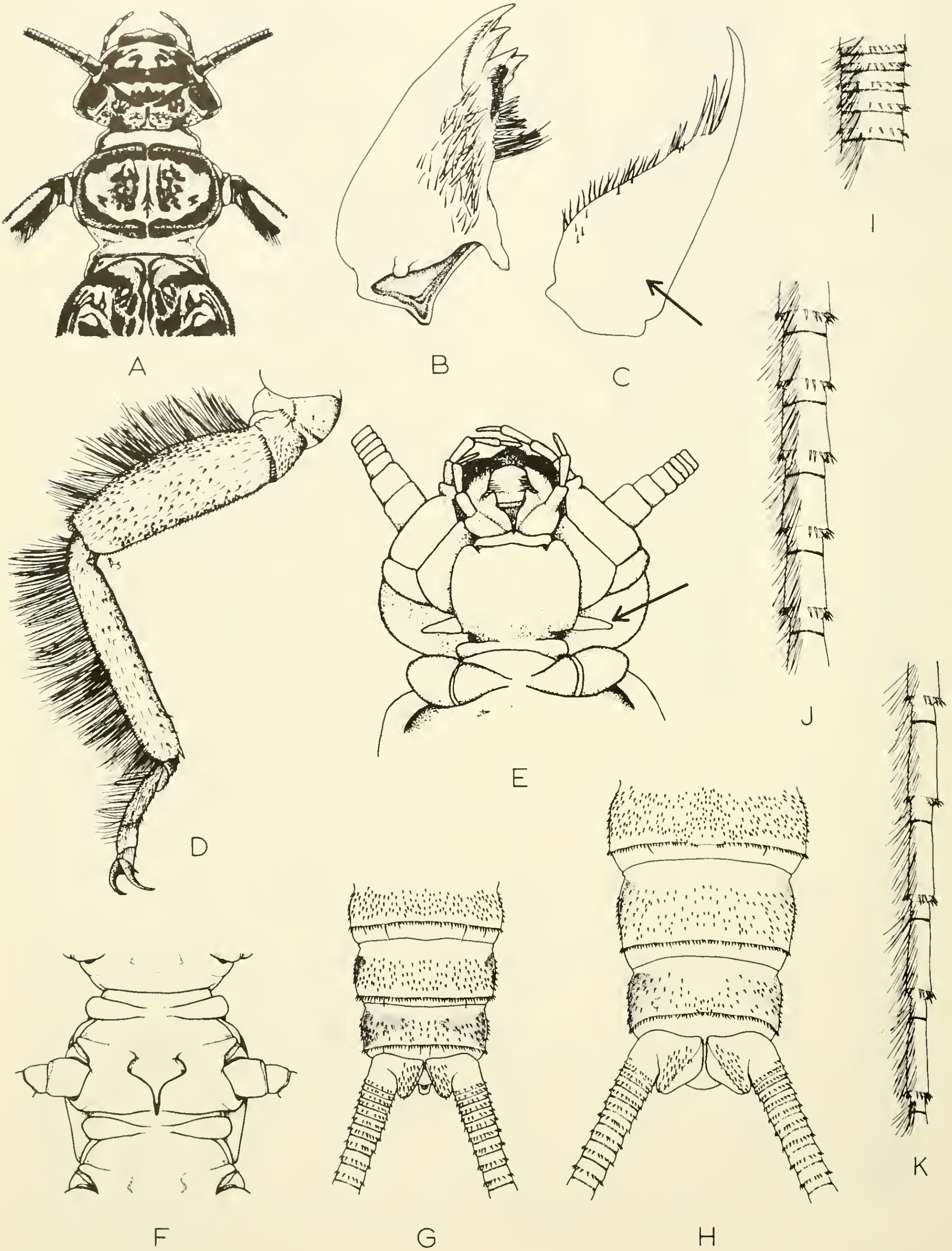

Fig. 7. Nymphal characters of *Helopicus nalatus*: A, head, pronotum pattern; B, right mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

7 I–K). Posterior setal row of male 8th abdominal sternum uninterrupted mesally (Fig. 7 G); setal row of female interrupted mesally (Fig. 7 H).

Nymph biology.— Poorly known, *H. nalatus* collected as nymphs from late Jan.–May (Frison 1942), primarily in debris and leaf packs in Arkansas (J. Feminella and K. Stewart, unpubl. data).

North American species list/distribution.— (1) *Helopicus bogaloosa* Stark & Ray — FLA, GA, LA, MS, (2) *H. nalatus* — ARK, IND, KAN, MICH, MO, OK, (3) *H. subvarians* (Banks) — CONN, FLA, MAINE, NC, ONT, PA, QUE, SC, TN, VA, WV.

Hydroperla Frison

Type species.— *Hydroperla crosbyi* (Needham & Claassen).

Previous nymph descriptions/illustrations.— (1) *H. crosbyi* — Frison (1935; labrum, mandible, maxilla, labium, mentum, submentum, habitus), Ross and Frison (1937), Ricker (1952), Stewart et al. (1976; mesosternal Y-arms), Oberndorfer and Stewart (1977; 1st instar habitus, mouthparts), Ray and Stark (1981; mandible, lacinia, labrum), Shepard and Stewart (1982; gills), (2) *H. fugitans* — Frison (1935; habitus, labrum, mandible, maxilla, labium, mentum, submentum), Ray and Stark (1981; labrum, mandible, lacinia), (3) *H. phormidia* — Ray and Stark (1981; habitus, labrum, mandible, lacinia).

Nymph description.— (*H. crosbyi*) (Figs. 8 A–K). Body and legs yellow with brown markings; antennae and cerci yellow. Head with wide M-band between antennal bases, enclosing 3 yellow spots; yellow M-band anterior to median ocellus and brown transverse band anterior to it; 2 irregular brown marks behind eyes, enclosing sinuate band of spinules 2–3 wide; occipital spinule band interrupted by wide mesal space (Fig. 8 A). Laciniae triangular, bidentate, with row of 16–20 marginal setae, 4–6 submarginal setae, 2 axillary setae and well-developed median ventral patch of 10–12 setae; terminal tooth about 0.25 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Fig. 8 C). Left mandible without deep cleft, distinct serrations of teeth or median ventral setal patch; band of acanthae from base of dorsal teeth to marginal setae (Fig. 8 B). Prominent submental gills, projecting portion about 2.0–2.5 times their basal diameter (Fig. 8 E). Pronotum encircled with wide brown band except for narrow light lateral margins; complete marginal row of short setae (Fig. 8 A). Y-arms of mesosternum meet posterior corners of furcal pits (Fig. 8 F). Wingpads with anterior brown markings, with M-shaped mesal mark, and flat posterior U-mark; short setae on all margins (Fig. 8 A). Femora with median dorsal, longitudinal, dark bar, numerous short spinules and dorsal fringe of silky, yellow hairs; tibiae/tarsi with silky, yellow hair fringe (Fig. 8 D). Abdominal terga with anterior, transverse brown band and posterior brown margin; short posterior setal fringe and numerous (> 50) intercalary spinules. Cercal segments with apical whorl of short setae and complete dorsal fringe of silky, yellow hairs (Figs. 8 I–K). Posterior setal row of male 8th abdominal sternum uninterrupted mesally (Fig. 8 G); 8th sternal setal row of female interrupted mesally (Fig. 8 H).

Nymph biology.— Well known for *H. crosbyi*. Early instars appear in late Oct. in Texas, after an approximate 7-month egg diapause. They grow rapidly through the winter and emerge in Feb.–Mar. Male and female nymphs have an estimated 12 and 14 instars, respectively. Nymphs are carnivorous, feeding primarily on Chironomidae and Simuliidae larvae, and mayfly nymphs (Oberndorfer and Stewart 1977). Found in permanent and intermittent streams throughout the Mississippi Valley, southward to Arkansas, Oklahoma, and Texas, in debris, leaf packs and cobble-gravel riffle substrate (Frison 1935, Szczytko and Stewart 1977). Brief notes were given by Frison (1935) on the biology of *H. fugitans* (as *H. harti*) that indicated its life cycle and food habits are similar to *H. crosbyi*. *H. phormidia* occurs in brown-water coastal rivers in Northwest Florida, in leaf packs associated with blue-green algae; it feeds on Chironomidae and Similiidae larvae and emerges in Mar.–Apr., based on field collections of exuviae, the single field-collected adult male, and laboratory rearings of a male and female (Ray & Stark 1981).

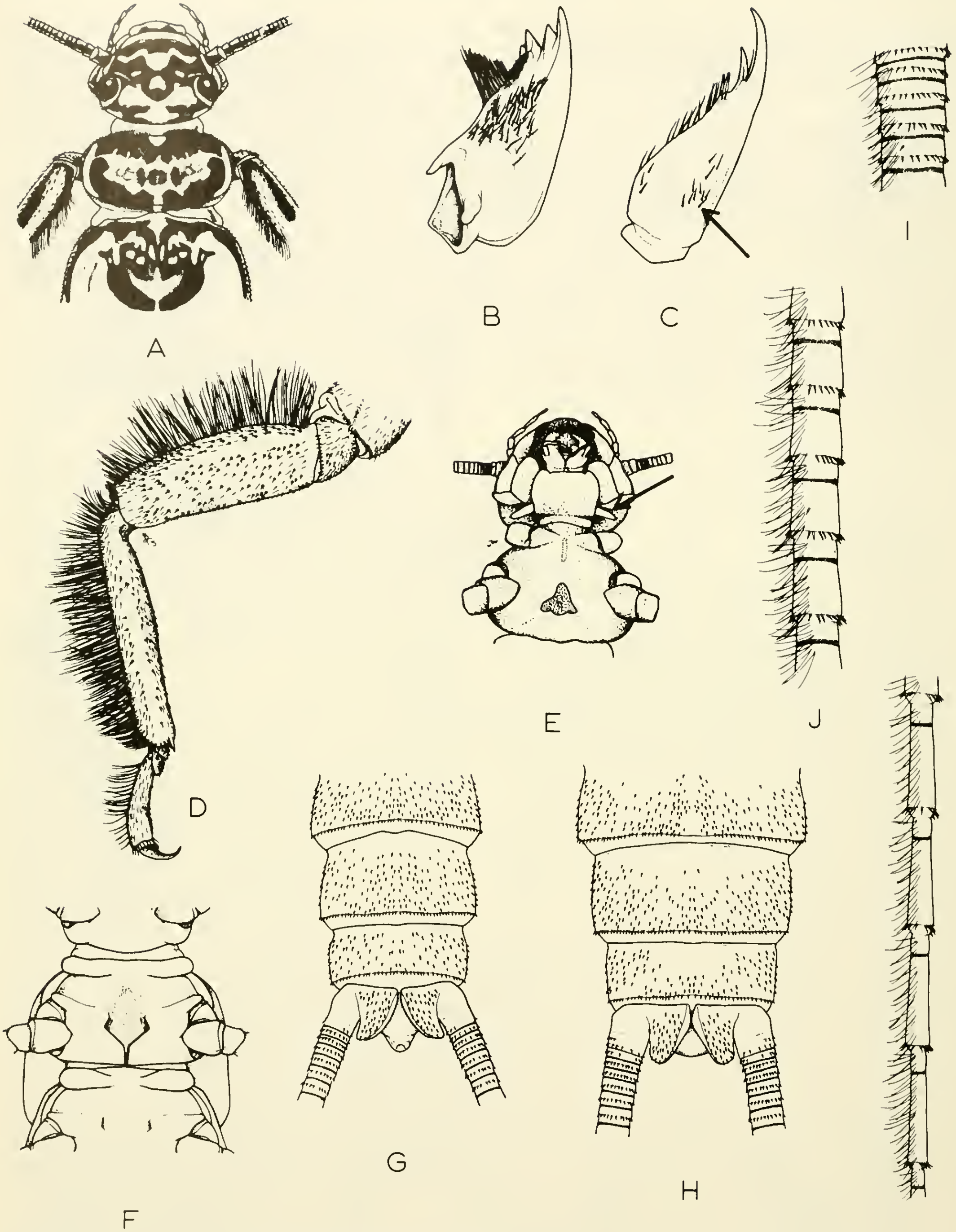

Fig. 8. Nymphal characters of *Hydroperla crosbyi*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

North American species list/distribution.— (1) *Hydroperla crosbyi* — ARK, ILL, IND, KAN, OK, MO, TX, (2) *H. fugitans* (Needham & Claassen) — ARK, ILL, IND, KAN, TN, TX, (3) *H. phormidia* Ray & Stark — FLA.

Isogenoides Klapálek

Type species.— *Isogenoides frontalis* (Newman).

Previous nymph descriptions/illustrations.— (1) *I. colubrinus* — (possibly Claassen 1931), (2) *I. doratus* — Frison (1942; habitus, mandible, maxilla, labium), (3) *I. elongatus* — Ricker (1952; mandible), Baumann et al. (1977; lacinia), (4) *I. frontalis* — Frison (1942; habitus, mandibles, maxilla, labium), Hilsenhoff and Billmyer (1973; lacinia), (5) *I. hansoni* — Ricker (1952; habitus, mandibles, labium), (6) *I. krumholzi* — none, (7) *I. olivaceus* — Frison (1942; habitus, mandibles, maxilla, labium), Hilsenholff and Billmyer (1973; lacinia), (8) *I. varians* — Ross and Frison (1937; habitus), (9) *I. zionensis* — Ricker (1952), Baumann (1973; habitus, maxillae, mandibles), Baumann et al. (1977; labrum, labium with gills, maxilla, mandible, mesosternal ridge pattern), Shepard and Stewart (1982; gills—text and illustrations of *frontalis* are actually *zionensis*).

Nymph description.— (*I. zionensis*). Body yellow with light brown markings; antennae, legs yellow, cerci brown; thin rows of long, light, silky hairs along middorsal line of thorax and abdomen. Head with yellow M-mark forward of anterior ocellus; ocellar triangle enclosing a brown spot; occiput with large yellow spots, enclosed by brown, well-developed row of occipital spinules, interrupted mesally (Fig. 9 A). Laciniae triangular, bidentate with a distinct knob below subapical tooth; complete row marginal setae and scattered submarginal setae in 3 groups of 2 or 3 setae each; 2 or 3 axillary setae; terminal tooth about 0.35 total outer lacinial length, and subapical tooth about 0.5 length of terminal tooth (Fig. 9 C). Left mandible without deep cleft or median ventral patch of setae; distinct serrations on ventral tooth; row of acanthae at base of dorsal teeth (Fig. 9 B). Prominent submental gills, projecting portion about 3 times their basal diameter (Fig. 9 E). Pronotum with faint reticulate light brown pattern, a narrow anterior transverse dark band, posterior brown margin and light lateral margins; anterior and posterior marginal row of short setae, sometimes with 2 or 3 longer setae on corners. Y-arms of mesosternum reach posterior corners of furcal pits; a distinctive median longitudinal ridge connecting fork of Y with a transverse ridge (Fig. 9 F). Meso-metanota with pairs of large round anteromesal light spots and faint pattern; stout spinules on anterior margins, and scattered in darker pigmented areas. Legs with short, stout setae and dense dorsal fringe of silky, yellow hairs (Fig. 9 D). Abdominal terga light brown, somewhat darker anteriorly, with more than 100 stout intercalary spinules and posterior row of short, stout setae. Posterior setal row of male 8th abdominal sternum uninterrupted mesally (Fig. 9 G); setal row of female 8th sternum interrupted mesally, and often notched (Fig. 9 H). Cercal segments with apical whorl of short, stout setae; cerci with complete dorsal fringe of silky, yellow hairs (Figs. 9 I–K).

Nymph biology.— Poorly known except brief notes for the eastern *I. frontalis* and western *I. zionensis*. We have found *I. zionensis* nymphs in small, clear, rock-bottomed creeks and large silty rivers in Colorado and Utah; they are often the only large perlodids in lower reaches of rivers (Baumann et al. 1977). Mature *I. zionensis* nymphs are found in May in Colorado. Adults have been collected in late May in Utah (Baumann 1973) and Jun. in the Northwest Territories (Ricker 1955). Baumann et al. (1977) gave emergence times for *I. colubrinus* and *I. elongatus* as Mar.–Aug. and May–Jun., respectively. Hilsenhoff and Billmyer (1973) and Dosdall and Lemkuhl (1979) reported univoltine life cycles for *I. frontalis* in Wisconsin and Saskatchewan, based on collections of uniformly large nymphs in May, emergence in May–Jun. and appearance of early instars in early Aug. Harper and Pilon (1975) reported emergence in Jul.–Aug. in northern Quebec, and Shapas and Hilsenhoff (1976) found larval Chironomidae and other Diptera in the guts of nymphs.

North American species list/distribution.— (1) *Isogenoides colubrinus* (Hagen) — ALAS, ALB, BC, COL, ID, MANIT, MONT, NWT, SASK, UT, WYO, YUK, (2) *I. doratus* (Frison) — IOW, MICH, PA, QUE, (3) *I. elongatus* (Hagen) — ALB, ARIZ, BC, COL, ID, MONT, NM, UT, WN, WYO, (4) *I. frontalis* — LAB, MANIT, MICH, MINN, NF, NY, QUE, SASK, WISC, (5) *I. hansoni* (Ricker) — CONN, MASS, MD, NEW BR, NC, NS,

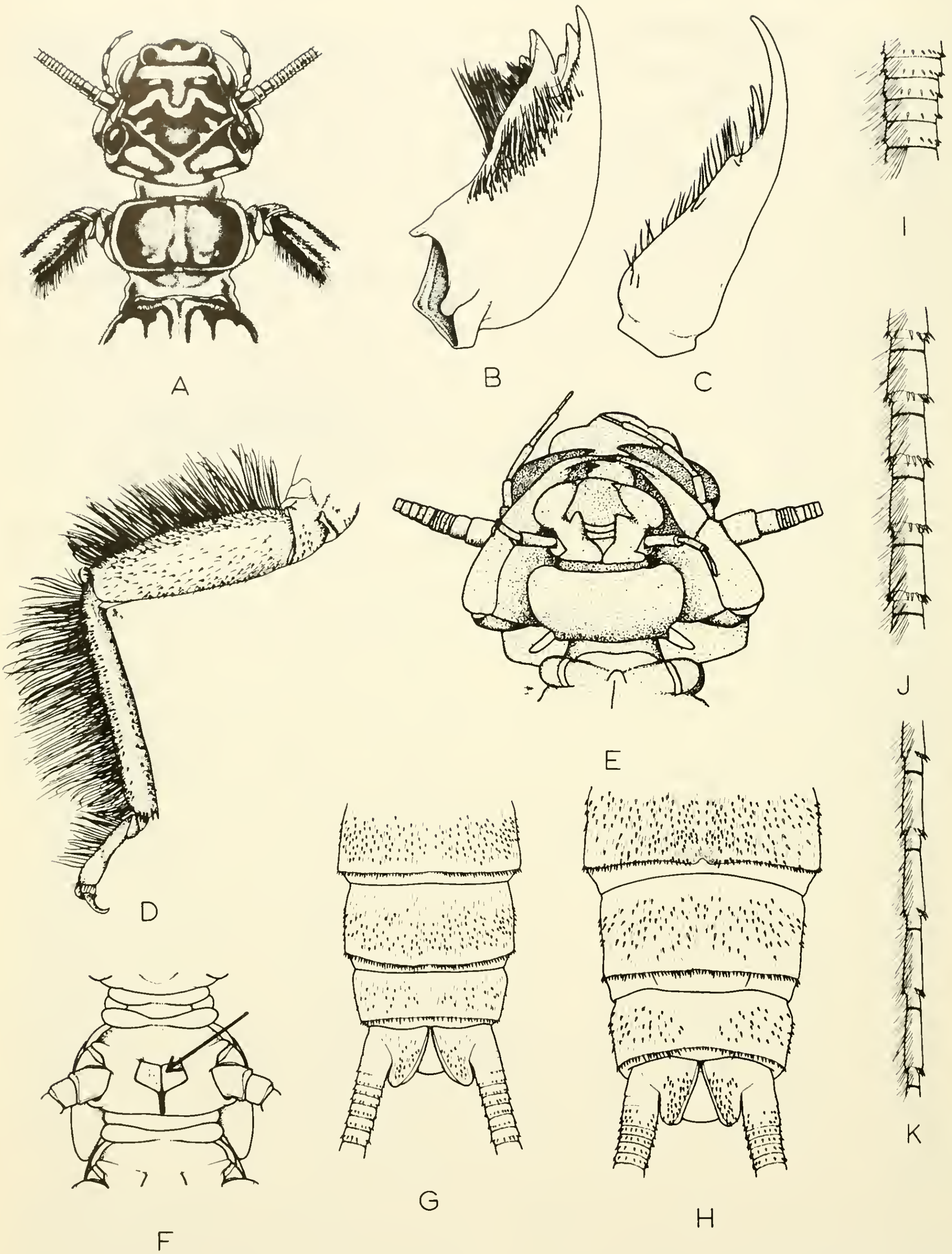

Fig. 9. Nymphal characters of *Isogenoides zionensis*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

NY, PA, QUE, VA, WV, (6) *I. krumholzi* (Ricker) – MICH, MINN, (7) *I. olivaceus* (Walker) – MICH, MINN, ONT, QUE, WISC, (8) *I. varians* (Walsh) – ILL, IND, MICH, MS, SC, TN, (9) *I. zionensis* – ALAS, COL, NM, NWT, UT.

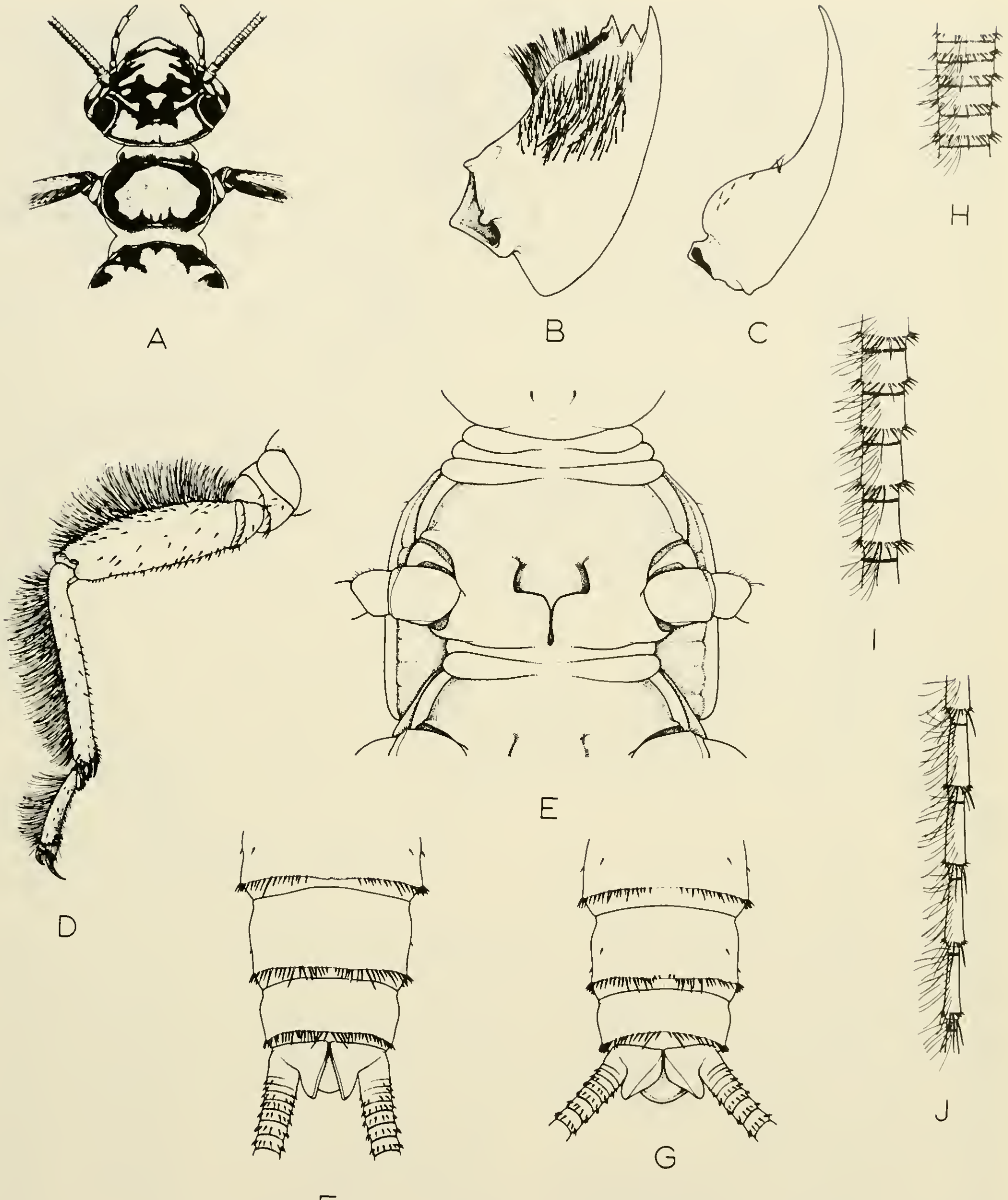

Fig. 10. Nymphal characters of *Kogotus nonus*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

Kogotus Ricker

TYPE SPECIES.— *Kogotus nonus* (Needham & Claassen).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— (1) *K. alameda* — none, (2) *K. modestus* — Frison (1942; habitus, mandibles, maxilla, labium), (3) *K. nonus* — Ricker (1952), Baumann et al. (1977); no previous nymphal illustrations.

NYMPH DESCRIPTION.— (*K. nonus*) (Figs. 10 A–J). Body brown with dark brown markings; antennae, legs, cerci brown. Head with light M-pattern anterior to darker M, between antennae; light spot in ocellular triangle and 2 small light spots outside lateral ocelli; occiput light, without spinule row (Fig. 10 A). Laciniae unidentate with 6–8 submarginal setae scattered along basal half (Fig. 10 C). Left mandible without deep cleft, serrations of teeth or median patch of ventral setae; row of acanthae along base of dorsal teeth (Fig. 10 B). Gills absent. Pronotum light, encircled with brown band, except light lateral margins; a few tiny marginal spinules, but mostly glabrous (Fig. 10 A). Y-arms of meso-sternum meet posterior corners of furcal pits; no transverse anterior suture connecting furcal pits (Fig. 10 E) as in *Rickera sorpta* (Fig. 19 E). Meso-metanota with indistinct markings mostly glabrous (Fig. 10 A). Legs brown with stout, sharp setae and dorsal fringe of silky, golden hairs (Fig. 10 D). Abdominal terga with posterior fringe of stout, sharp setae, longest mesally; segments 1–5, with fewer than 5 intercalary spinules, if present, and segments 6–10, with 10 or fewer intercalary spinules. Both male and female 8th abdominal sternae with meso-posterior interruption of posterior setal row (Figs. 10 F, G). Cercal segments with apical whorl of short, stout setae, and cerci with dorsal fringe of silky, golden hairs (Figs. 10 H–J).

NYMPH BIOLOGY.— Poorly known for *K. nonus* except that nymphs are rare in some intensively studied streams (Sheldon and Jewett 1967, Kerst and Anderson 1974) and emerge Apr.–Sep. (Jewett 1959, Sheldon and Jewett 1967, Gaufin et al. 1972, Baumann et al. 1977). *K. modestus* (Banks) is univoltine in Colorado; final instars are present through Aug. and feed primarily on Chironomidae and mayflies (Allan 1982).

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— (1) *Kogotus alameda* (Needham & Claassen) — CAL, (2) *K. modestus* (Banks) — BC, COL, ID, MONT, NM, UT, WYO, (3) *K. nonus* — BC, CAL, ID, MONT, ORE, WN, WYO.

Malirekus Ricker

TYPE SPECIES.— *Malirekus hastatus* (Banks).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— Claassen (1931; labrum, mandibles, maxillae, labium, leg, habitus), Frison (1942), Ricker (1952), Ricker (1959; submental gills, mesosternal ridge), Shepard and Stewart (1983; gills).

NYMPH DESCRIPTION.— (Figs. 11 A–K). Body brown with dark brown markings; antennae, legs, cerci light brown. Head mostly brown with light M-mark forward of anterior ocellus; two light, ovate spots lateral to ocellular triangle, and light interocellar spot; two large ovate occipital spots, broken by reticulate brown lines and bordered behind by row of short, blunt spinules (Fig. 11 A). Laciniae bidentate, with clump of about 8 stout marginal setae located on slight knob below subapical tooth, and 4–5 scattered setae along middle inner margin; 2 or 3 scattered, short, stout submarginal setae, 2–3 axillary setae and dense median ventral patch of over 60 black clothing setae; terminal tooth about 0.35 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Fig. 11 C). Left mandible without deep cleft, serrations of teeth or median ventral setal patch (Fig. 11 B). Projecting portion of submental gills about 2 times their basal diameter (Fig. 11 E). Pronotum mostly light with reticulate dark pattern and dark clothing hairs; margins without setae (Fig. 11 A). Y-arms of mesosternum meet posterior corners or furcal pits (Fig. 11 F). Meso-metanota with anterior and posterior mesal triangulate light spots, and pair of central triangulate spots. Femora with 2 longitudinal narrow brown bands, irregular sparse row of short spinules along base of fringe hairs, and very sparse intercalary dorsal spinules. Femora and tibiae with dense fringe of white, silky hairs (Fig. 11 D). Abdominal terga brown with faint mesal, longitudinal, darker band and short, dark clothing hairs; fewer than 10 short intercalary spinules, and posterior fringe of very short setae. Cercal segments with apical whorl of short setae and dorsal fringe of silky, white hairs (Figs. 11 I–K). Posterior setal row of male 8th abdominal sternum with narrow mesal interruption (Fig. 11 G); 8th sternal setal row of female with wide mesal gap associated with developing subgenital plate (Fig. 11 H).

NYMPH BIOLOGY.— Relatively poorly known, with only general reference. Abundant in small upland spring brooks (Claassen

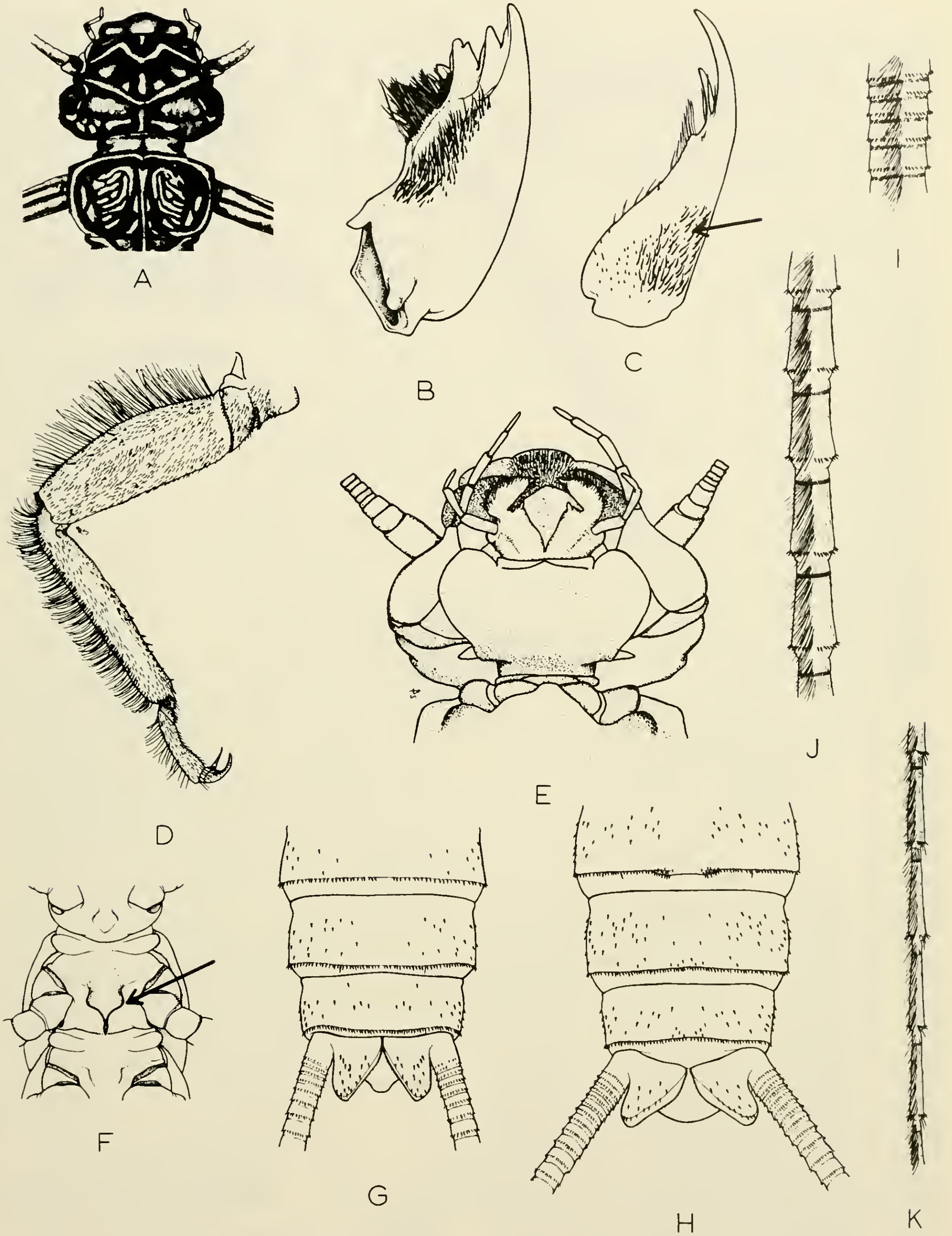

Fig. 11. Nymphal characters of *Malirekus hastatus*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

1931), small Appalachian streams (Ricker 1952), 1st to 3rd order streams in ridge and valley, and Blue Ridge provinces of Virginia (Kondratieff and Voshell 1982). Adults active Apr.–early Jun. (Kondratieff and Voshell 1982).

North American species list/distribution.— Monospecific genus; *M. hastatus* — GA, KY, MAINE, NC, NY, QUE, SC, TN, VA, WV.

Megarcys Klapálek

Type species.— *Megarcys ochracea* Klapálek.

Previous nymph descriptions/illustrations.— Only nymphs of *M. signata* have been described—Claassen (1931), Ricker (1943; habitus, labium, maxilla), Gaufin (1966; mesosternum), Cather & Gaufin (1975), Baumann et al. (1977; mesosternum).

Nymph description.— (*M. signata*) (Figs. 12 A–K). Body light brown with dark markings, and covered with short, dark clothing hairs; with mesal, longitudinal band of sparse, erect, silky, white hairs on thorax and abdomen and behind arms of ecdysial suture on head. Head mostly dark with light M-pattern forward of anterior ocellus, small light round spots lateral to ocellar triangle, light interocellar area, and nearly complete mesal longitudinal light band; ovate light occipital spots inside eyes, broken by reticulate brown lines and bordered behind by row of spinules (Fig. 12 A). Laciniae bidentate, with complete row of about 20 marginal setae along apical ⅔ of inner margin, a row of about 15 submarginal setae, 2 or 3 axillary setae, and no median ventral patch of setae; terminal tooth about 0.4 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Fig. 12 B). Left mandible without deep cleft; ventral tooth with prominent serrations, and median ventral patch of 4 setae (Fig. 12 C). Long submental gills, and a pair of curved simple gills located anterior supracoxal, anterior thoracic$_2$ and anterior thoracic$_3$ (Fig. 12 F). Pronotum mostly dark with reticulate light markings; darker areas covered by dark clothing hairs; a few short marginal spinules, but marginal setae absent (Fig. 12 A). Y-arms of mesosternum meet anterior corners of furcal pits (Fig. 12 F). Meso-metanota with light vase-shaped mesoposterior marking and pair of irregular ovate light spots; covered with dark clothing hairs. Dorsal surface of femora with dark clothing hairs, except on a mesal longitudinal band, and row of spinules at base of fringe hairs; femora and tibiae with dorsal fringe of silky, white hairs (Fig. 12 D). Abdominal terga brown with dense intercalary spinules and a posterior fringe of short spinules; faint pairs of small, light spots mesally and laterally. Cercal segments with apical whorl of short setae, and dorsal fringe of silky, white hairs (Figs. 12 I–K). Posterior setal row of male 8th abdominal sternum with mesal interruption (Fig. 12 G); posteromedian portion of female 8th sternum modified in shape and setal pattern (Fig. 12 H).

Nymph biology.— Known only for *M. signata* that has a univoltine life cycle (Cather and Gaufin 1975, Allan 1982), with early instars appearing in Jul.–Oct., depending on elevation, then exhibiting a generally slow growth pattern. Most rapid growth occurs during summer (Allan 1982), and fall and early spring, correlating with greatest carnivory (Cather and Gaufin 1975). Nymphs are omnivorous (Cather and Gaufin 1975, Allan 1982), feeding primarily on diatoms, chironomids, and mayflies (Richardson and Gaufin 1971, Cather and Gaufin 1975, Peckarsky 1980, Peckarsky and Dodson 1980, Allan 1982). Nymphs prefer swift, aerated, stony-bottomed habitats in higher elevation streams (Dodds and Hisaw 1925, Knight 1965, Knight and Gaufin 1966, Stark et al. 1975). Adults emerge Apr.–Jul. (Gaufin et al. 1966, Cather and Gaufin 1975, Allan 1982).

North American species list/distribution.— (1) *Megarcys irregularis* (Banks) — BC, WN, (2) *M. signata* — ALAS, BC, COL, ID, MONT, NEV, NM, UT, WYO, (3) *M. subtruncata* Hanson — BC, ID, MONT, ORE, WN, (4) *M. watertoni* (Ricker) — ALB, BC, ID, MONT, (5) *M. yosemite* (Needham & Claassen) — CAL, WN.

Oconoperla Stark & Stewart

Type species.— *Oconoperla weaveri* Stark & Stewart.

Previous nymph descriptions/illustrations.— Stark and Stewart (1982a; habitus, abdominal tergum 8 and detail of its setation, right mandible, lacinia, foreleg and magnified detail of its anterior aspect, basal antennal segments and detail of their setation. All illustrations SEMs except habitus.)

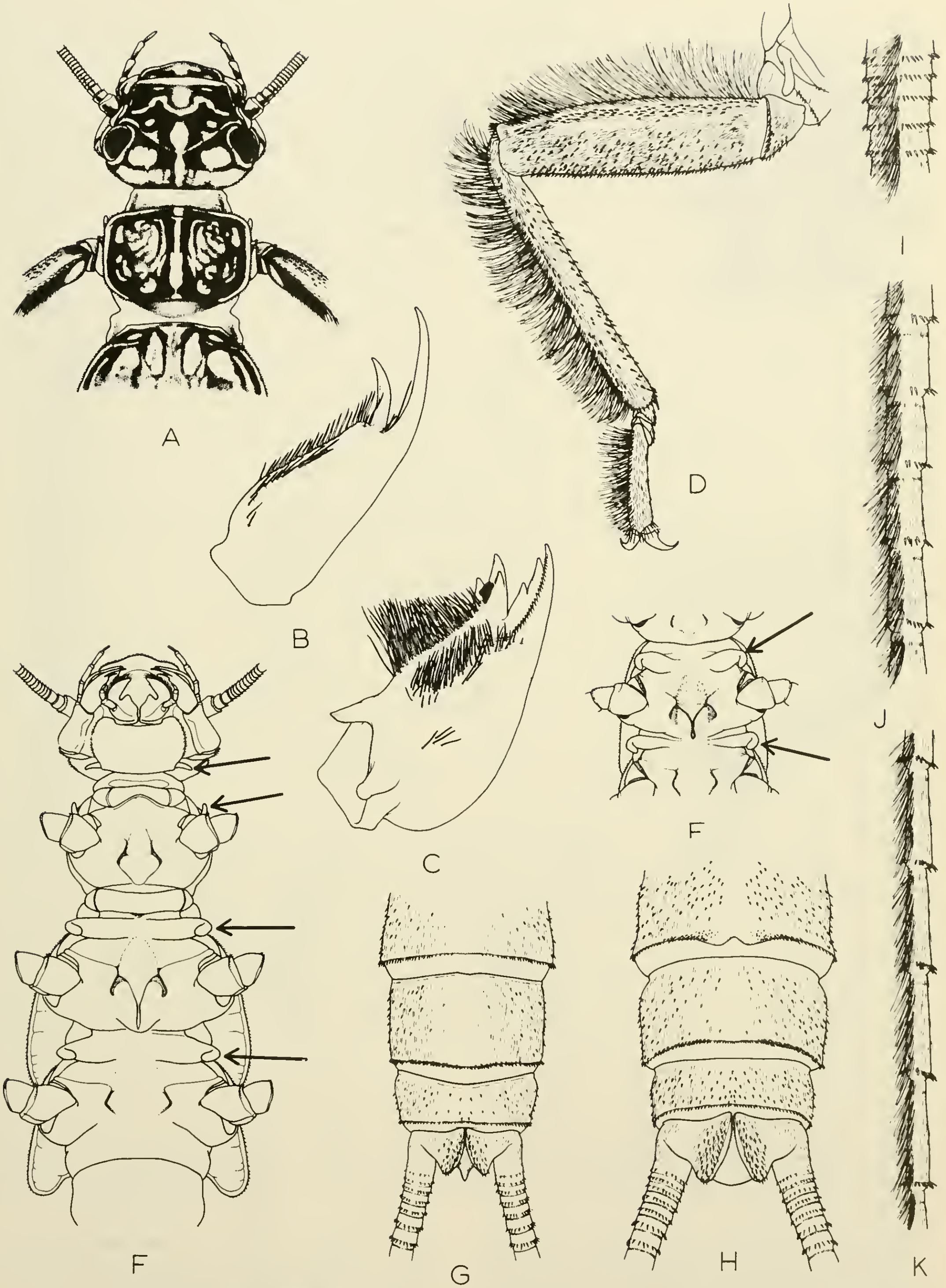

Fig. 12. Nymphal characters of *Megarcys signata*: A, head, pronotum pattern; B, left lacinia (ventral); C, left mandible (ventral); D, right front leg (anterior); E, submental and thoracic gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

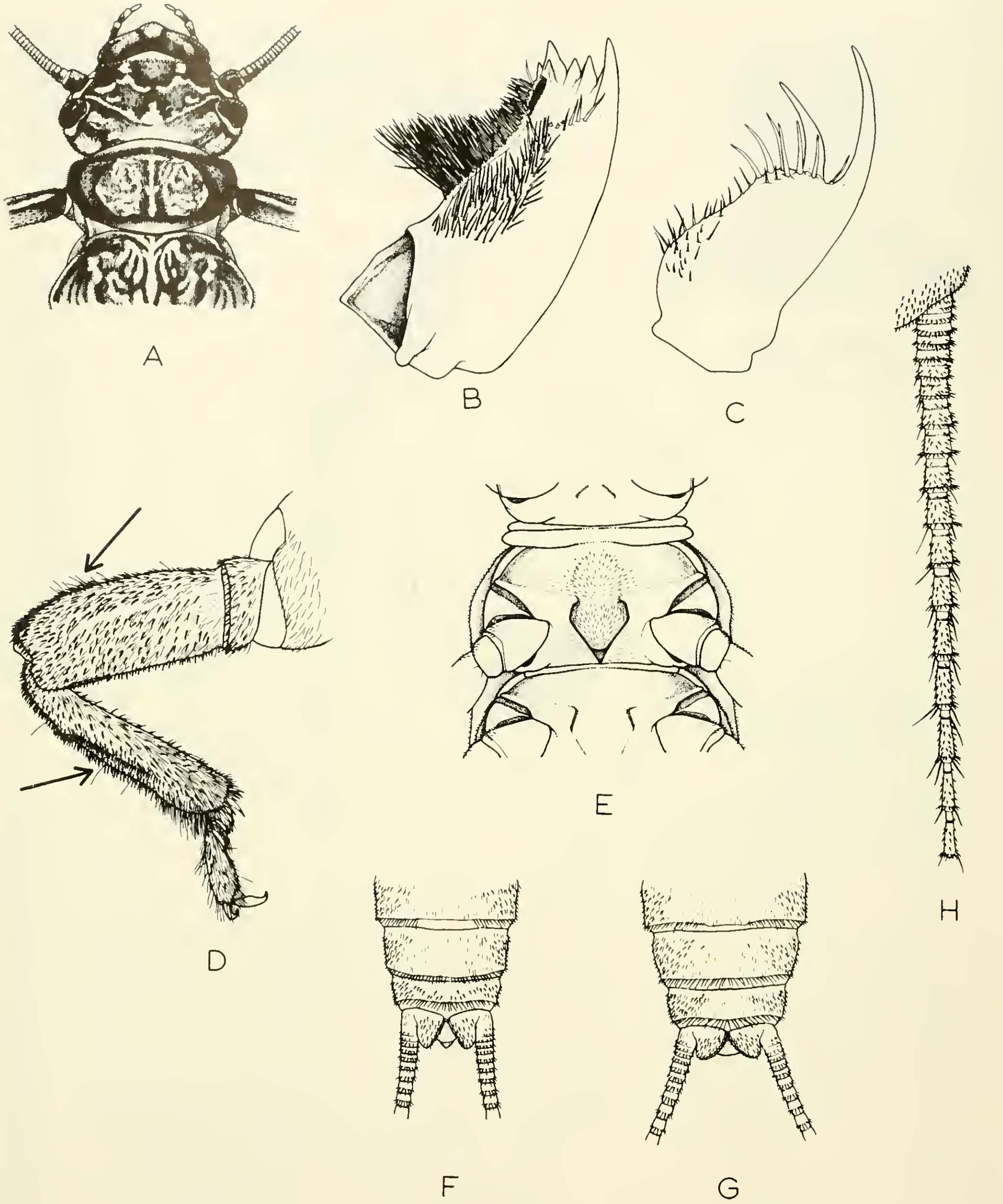

Fig. 13. Nymphal characters of *Oconoperla weaveri*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, right cercus (dorsal).

NYMPH DESCRIPTION.— (Figs. 13 A–H). Body brown, patterned with yellowish brown and covered with dark, wavy clothing hairs; membranous areas with purple-red pigment in living specimens; antennae, cerci yellowish brown. Head brown with pale M-mark forward of anterior ocellus; pair of small, irregular light spots anterior and posterior to M-mark; light spot in interocellar triangle; occiput dark, with reticulate light markings; occipital spinules absent (Fig. 13 A). Laciniae bidentate with about 4–6 robust setae on a low shoulder below subapical tooth, followed by about 12 marginal setae; 2 or 3 scattered submarginal setae and patch of 14–16 short, stout submarginal setae in basal half, and an axillary seta; setae absent from median ventral surface; terminal tooth about 0.4 total outer lacinial length, and strongly diverging subapical tooth about 0.7 length of terminal tooth (Fig. 13 C). Left mandible without deep cleft, serrations of teeth or median ventral setal patch; distinct row of acanthae near base of dorsal tooth, and 4 robust setae near base of ventral tooth (Fig. 13 B). Submental gills absent. Pronotum margined with short spinules and notched posterolaterally; its surface rugose and dark, with light reticulate pattern (Fig. 13 A). Y-arms of mesosternum meet posterior corners of furcal pits (Fig. 13 E). Mesometanota dark with light reticulate markings and covered with dark clothing hairs; margined laterally with short spinules (Fig. 13 A). Legs short, stout; outer (anterior) femoral surface brown with light, narrow longitudinal band, covered with socketed spinelike setae and wavy, dark clothing hairs; tibiae brown with setae and clothing hairs; no fringe of silky hairs on femora or tibiae (Fig. 13 D). Abdominal terga brown, with mesal and lateral rows of paired light spots; surface densely covered with short, thick, curled setae and dark, flat clothing hairs; no distinct posterior fringe of setae. Cercal segments with apical whorl of setae; no dorsal, erect hairs or silky fringe; each segment with 3–5 stout, erect, long, apical setae ventrally (Fig. 13 H). Posterior setal row of male and female 8th abdominal sternum interrupted (Figs. 13 F, G), slight indication of developing subgenital plate in female (Fig. 13 G).

Nymph biology.— Unknown, except habitat is under rocks in splash zones of small spring seeps in North and South Carolina (Stark and Stewart 1982).

North American species list/distribution.— Monospecific genus; *O. weaveri* — NC, SC.

Oroperla Needham

Type species.— *Oroperla barbara* Needham.

Previous nymph descriptions/illustrations.— Needham (1933; habitus), Ricker (1952; mandible, maxilla), Shepard and Stewart (1983; ventral habitus, gills).

Nymph description.— (Figs. 14 A–K). Body light brown with brown markings; dorsal surfaces covered with short, dark clothing hairs; erect white, silky hair fringe behind arms of ecdysial suture on head and as mesal longitudinal band on thorax and abdomen (Fig. 14 A); antennae brown, legs and cerci yellowish brown. Head mostly brown with pale and often interrupted, narrow, light M-mark forward of anterior ocellus; indistinct light spot in interocellar space and paired light occipital spots broken by reticulate dark lines; no occipital spinule row (Fig. 14 A). Laciniae triangulate, bidentate, with complete fringe of long inner marginal setae on apical ⅔; 2 patches of submarginal setae at each end of marginal fringe; no median ventral patch of setae; terminal tooth about 0.4 total outer lacinial length and subapical tooth 0.5 length of terminal tooth (Fig. 14 B). Left mandible moderately cleft with large denticles on ventral tooth; median ventral setae absent (Fig. 14 C). Gills as follows: submental, short, simple anterior thoracic$_1$, double anterior thoracic$_2$ and AT$_3$, and simple ventrolateral on abdominal segments 1–7 (Fig. 14 D). Pronotum with about even light and dark reticulate pattern and no marginal setae (Fig. 14 A). Y-arms of mesosternum meet posterior corners of furcal pits (Fig. 14 F). Mesometanota with even, light and dark reticulate pattern, and no marginal setae or spinules (Fig. 14 A). Femora and tibiae without intercalary setae or spinules; covered with dark, wavy clothing hairs; with dense fringe of white, silky hairs (Fig. 14 E). Abdominal terga light brown with pairs of mesal and lateral small dark dots, and surface covered with minute dark freckles; lateral surfaces of gilled segments (Ab$_{1\text{-}7}$) are highly rugose; no apical tergal fringe of setae or intercalary spinules. Cercal segments with apical whorl of short setae and dense dorsal fringe of silky, white hairs (Figs. 14 I–K). No posterior setal fringe on male and female 8th abdominal sternae (Figs. 14 G, H); male 8th sternum with straight posterior margin (Fig. 14 G), and female with concave posterior margin on 8th sternum (Fig. 14 H).

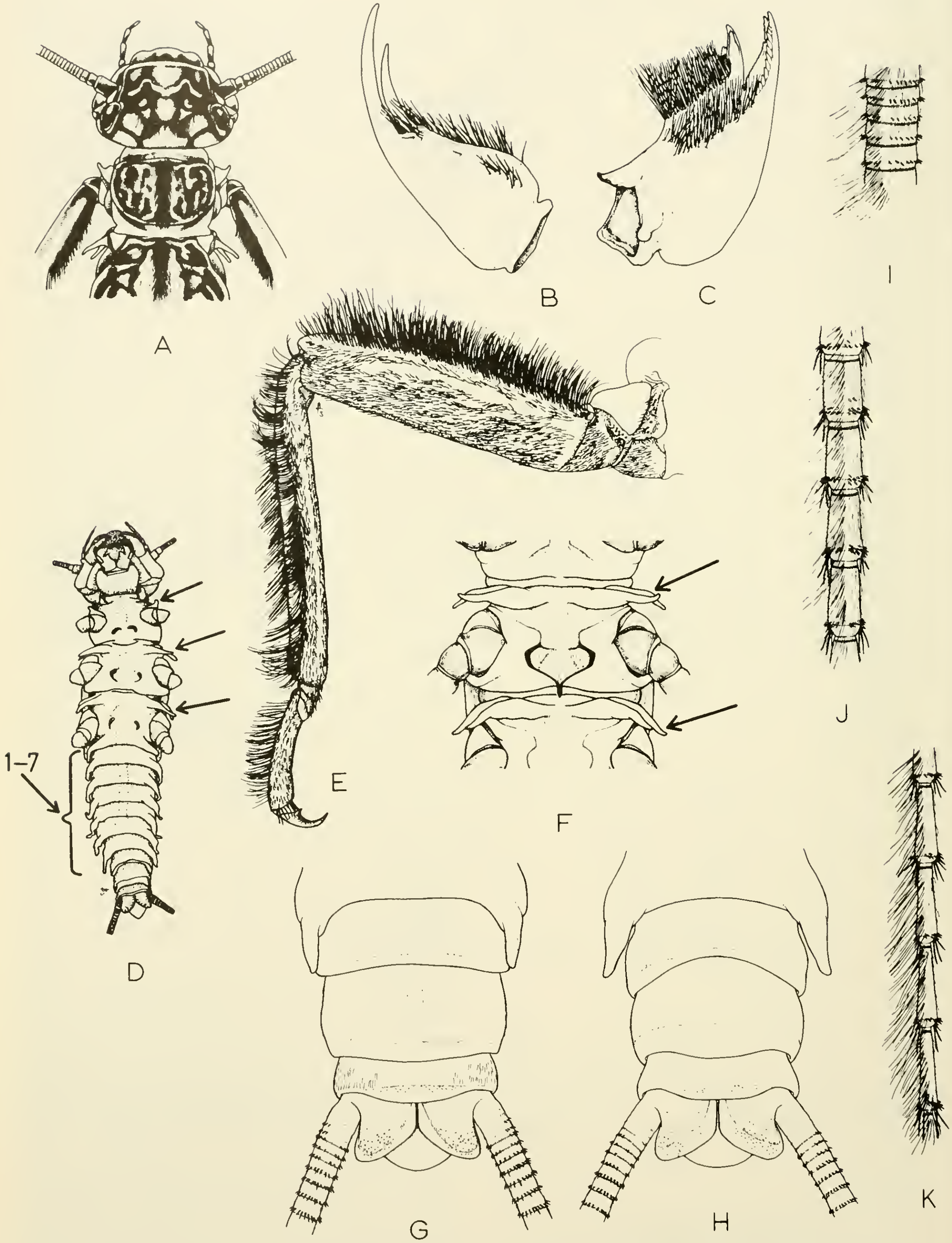

Fig. 14. Nymphal characters of *Oroperla barbara*: A, head, pronotum pattern; B, right lacinia (ventral); C, left mandible (ventral); D, ventrum, showing thoracic and abdominal gills; E, right front leg (anterior); F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

Nymph biology.— Relatively unknown. The species is apparently endemic to rivers of the Sierra Nevada Mts. of California (Ricker 1952, Jewett 1960, Jewett 1966). Nymphs collected in the Yuba river in March 1974 emerged in Apr.–May (Siegfried et al. 1977). Jewett (1966) observed captive nymphs ingesting smaller *Oroperla* and mayfly nymphs during the day.

North American species list/distribution.— Monospecific genus; *O. barbara* — CAL.

Osobenus Ricker

Type species.— *Osobenus yakimae* (Hoppe)

Previous nymph descriptions/illustrations.— Jewett (1955; labium, abdomen, head-pronotum, maxilla).

Nymph description.— (Figs. 15 A–J). Body yellow with dark brown pattern; antennae, legs yellow; cerci light brown. Head yellow, with broad U-shaped brown marking, sometimes broken on anterior frons by hint of a light M-marking; narrow dark bar from eye toward foramen, containing 4 or 5 spinules near eye (Fig. 15 A). Laciniae bidentate with 1 or 2 axillary setae, 2 marginal setae just below subapical tooth and 4 or 5 short submarginal setae; no setae on median ventral surface; terminal tooth 0.5 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Fig. 15 C). Left mandible without deep cleft, serrations of teeth, or median ventral setal patch; row of acanthae along inner base of dorsal tooth (Fig. 15 B). Gills absent. Pronotum encircled with broad brown band, leaving irregular diamond-shaped yellow center; no marginal setae or spinules (Fig. 15 A). Y-arms of mesosternum and transverse suture touch anterior corners of furcal pits (Fig. 15 E). Mesometanota with brown pigment bordering a central butterfly-shaped light spot; glabrous except for a few small anterior marginal setae (Fig. 15 A). Femora yellow with band of long setae at base of hair fringe, and scattered long anteroventral setae; dorsal fringe of yellow, silky hairs (Fig. 15 D). Tibiae with scattered stout intercalary setae and fringe of yellow, silky hairs (Fig. 15 D). Abdominal terga yellow with 2 broad longitudinal brown bands; pair of long intercalary setae on segments 1–9 and 2 pair on segment 10; well-developed posterior setal fringe with longest setae mesally. Cercal segments with apical whorl of stout setae and dorsal fringe of yellow hairs (Figs. 15 H–J). Posterior setal row of male 8th abdominal sternum narrowly interrupted mesally (Fig. 15 F); 8th setal row of female interrupted about 0.3 width of sternum (Fig. 15 G).

Nymph biology.— Unknown, except found in large creeks and rivers, emerging in late May–early Jul.

North American species list/distribution.— Monospecific genus; *O. yakimae* — BC, CAL, ORE, WN.

Perlinodes Needham & Claassen

Type species.— *Perlinodes aurea* (Smith).

Previous nymph descriptions/illustrations.— Ricker (1952), Baumann et al. (1977), Stark and Stewart (1982b; habitus, mandible, serrations of mandibular teeth, lacinia), Shepard and Stewart (1983; gills).

Nymph description.— (Figs. 16 A–K). Body brown, patterned with yellow and dorsal surfaces covered with short, stout spinules; tuft of erect, silky, yellow hairs on occiput and as mesal narrow band on thorax and abdomen (Fig. 16 A). Head mostly dark, with interrupted M-pattern forward of median ocellus, 2 light round spots lateral to ocellar triangle and light interocellar spot; 2 light round spots inside eyes, broken by dark reticulate lines; stout postocular spinules, occipital spinules not in a distinct row, continuous with other intercalary spinules of head (Fig. 16 A). Laciniae triangular, bidentate, with full fringe of marginal and submarginal setae, and distinct row of about 10 stout setae on low shoulder at base of apical tooth; no median ventral patch of setae; terminal tooth 0.3 total outer lacinial length and subapical tooth 0.67 length of terminal tooth (Fig. 16 B). Left mandible deeply cleft, with prominent serrations of teeth; median ventral patch of about 5 setae (Fig. 16 C). Paired simple gills present on submentum, anteroventral thorax, anterior supra-coxal$_1$, and anteroventral thorax$_{2,3}$ (Fig. 16 F). Pronotum brown with light mesal stripe and reticulate light markings; margined by short, stout spinules. Y-arms of mesosternum meet posterior

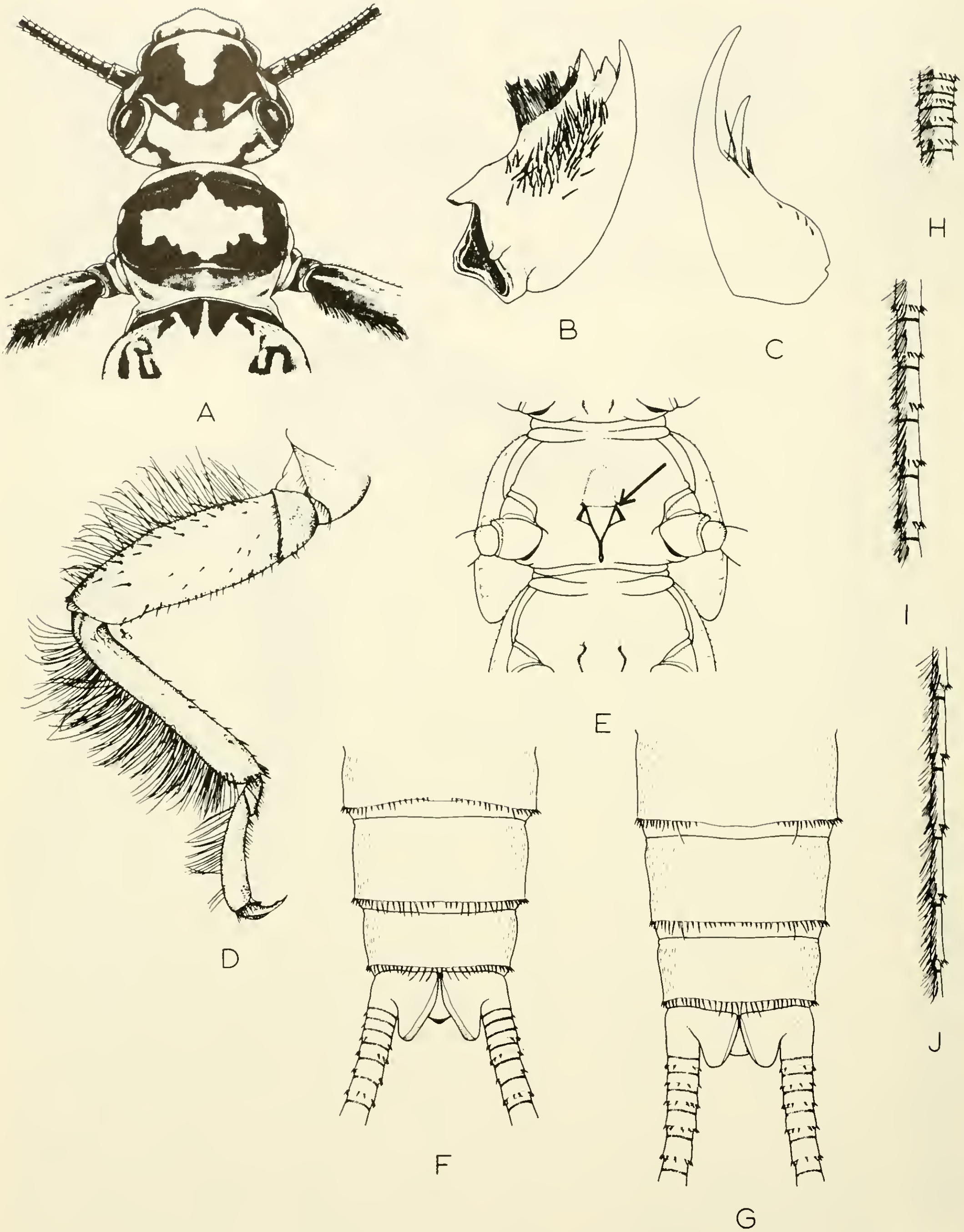

Fig. 15. Nymphal characters of *Osobenus yakamae*: A, head, pronotum pattern; B, left mandible (ventral); C, right lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

corners of furcal pits, and incomplete transverse arms reaching inward from anterior corners of furcal pits (Fig. 16 D). Meso-metanota with brown pigment bordering a central butterfly-shaped light spot; a few small anterior marginal setae. Femora mostly brown

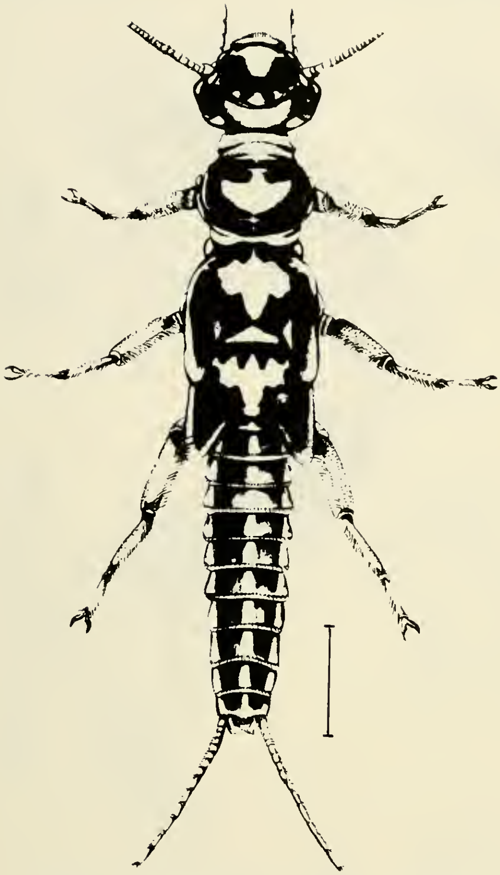

Fig. 15K. *Osobenus yakamae*: nymph habitus; scale line = 2 mm.

with light mesal longitudinal bar; stout spinules on brown areas, and dorsal fringe of yellow, silky hairs; tibiae with row of spinules at base of yellow, silky hair fringe and few dorsal intercalary spinules (Fig. 16 E). Abdominal tergae brown with mesal and lateral pairs of small yellow spots; dense intercalary spinules and posterior row of stout, dark brown spinules. Cercal segments dark brown, with apical whorl of stout spinules and dorsal fringe of silky, yellow hairs (Fig. 16 I–K). Posterior setal row and intercalary spinules of male 8th abdominal sternum interrupted (Fig. 16 G); female with developing subgenital plate and narrowly interrupted posterior setal row on 8th sternum (Fig. 16 H).

Nymph biology.— Relatively poorly known. Sheldon (1972) found *P. aurea* to be the rarest of the perlodid complex studied at Sagehen Creek, but the species displayed higher densities in lower reaches of the stream. Growth of nymphs was similar to other perlodids studied, but emergence was slightly earlier (Apr.–Jun.) than for other perlodids. Nymphs fed primarily on smaller Diptera found among periphyton.

North American species list/distribution.— Monospecific genus; *P. aurea* — ALB, CAL, ID, MONT, ORE, WN, WYO.

Pictetiella Illies

Type species.— *Pictetiella expansa* (Banks).

Previous nymph descriptions/illustrations.— Claassen (1931), Ricker (1952; maxilla), Baumann (1973; habitus, galea tip, left maxilla, left and right mandible), Baumann et al. (1977).

Nymph description.— (Figs. 17 A–I). Body yellow with light brown markings, sparse tufts of erect silky, yellow hairs behind ecdysial suture of head and as a mesal band on thorax and abdomen; antennae, legs yellow; cerci yellow basally, dark brown apically. Head with M-mark forward of anterior ocellus, small spots lateral to occellar triangle and largely light interocellar area; 2 large occipital yellow spots inside eyes, bordered behind by incomplete sinuate row of 8–10 spinules (Fig. 17 A). Laciniae triangular, bidentate, with 8–10 scattered marginal setae, about 8 submarginal setae, and 2 axillary setae; median ventral setal patch absent; terminal tooth about 0.45 total outer lacinial length and subapical tooth about 0.6 length of terminal tooth (Fig. 17 C). Left mandible not deeply cleft, teeth without distinct serrations, and no median ventral patch of setae (Fig. 17 B). Projecting portion of submental gills about 2 times their basal diameter (Fig. 17 E). Pronotum with reticulate pattern, nearly complete mesal light band, and light marginal border; marginal setae on anterior and posterior margins, longest on corners and absent on 0.5 of lateral margin (Fig. 17 A). Y-arms of mesosternum meet posterior corners of furcal pits (Fig. 17 F). Meso-metanota mostly dark with pair of light round spots; transverse spinule row along front ridge of wingpads, continuous with lateral marginal spinules (Fig. 17 A). Femora with band of stout setae along base of dorsal fringe and on anteroventral surface; dorsal fringe of golden, silky hairs (Fig. 17 D); tibiae with more than 50 dorsal intercalary spinules and

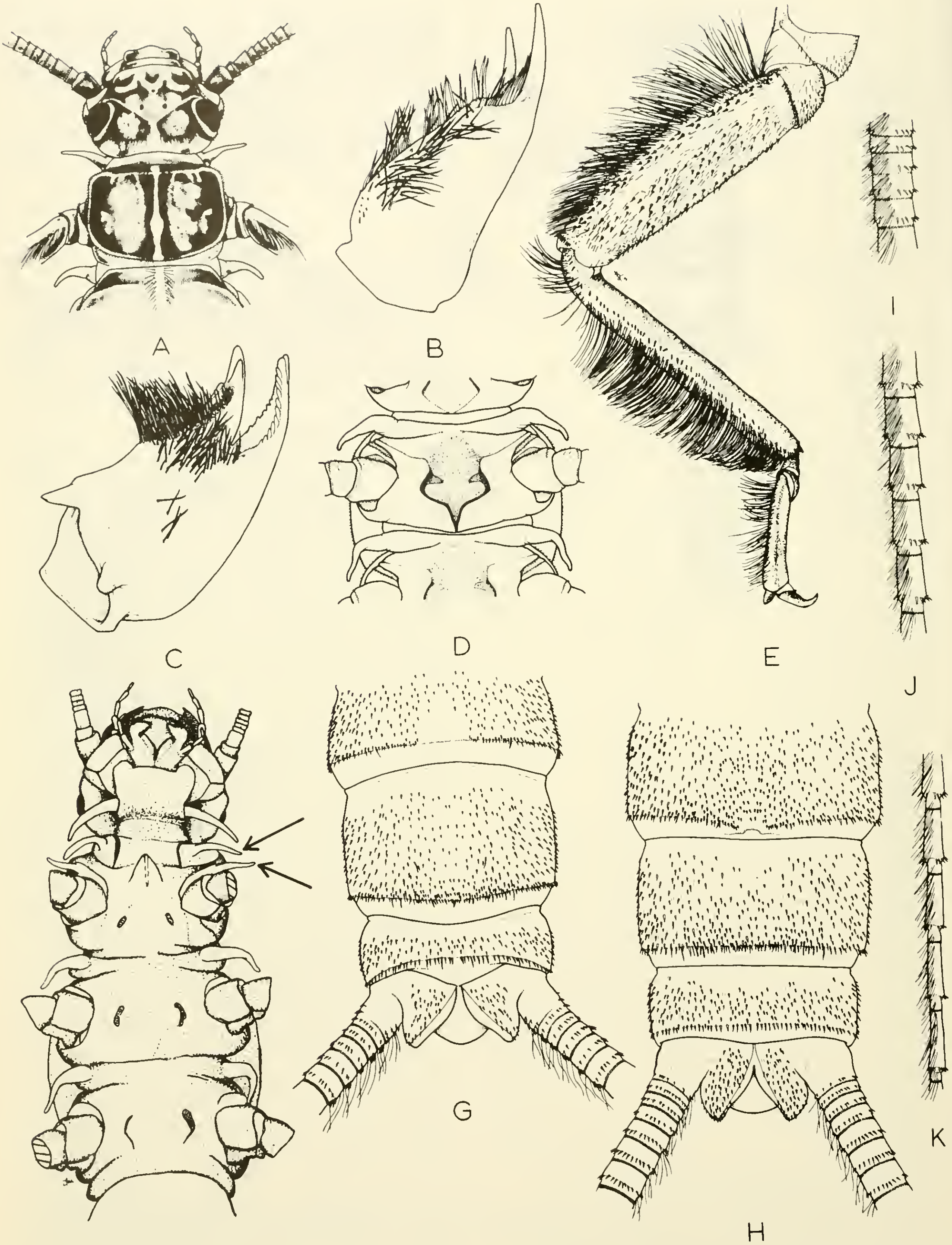

Fig. 16. Nymphal characters of *Perlinodes aurea*: A, head, pronotum pattern; B, left lacinia (ventral); C, left mandible (ventral); D, mesosternal Y-pattern; E, right front leg (anterior); F, submental, anterior thoracic, and thoracic gills; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

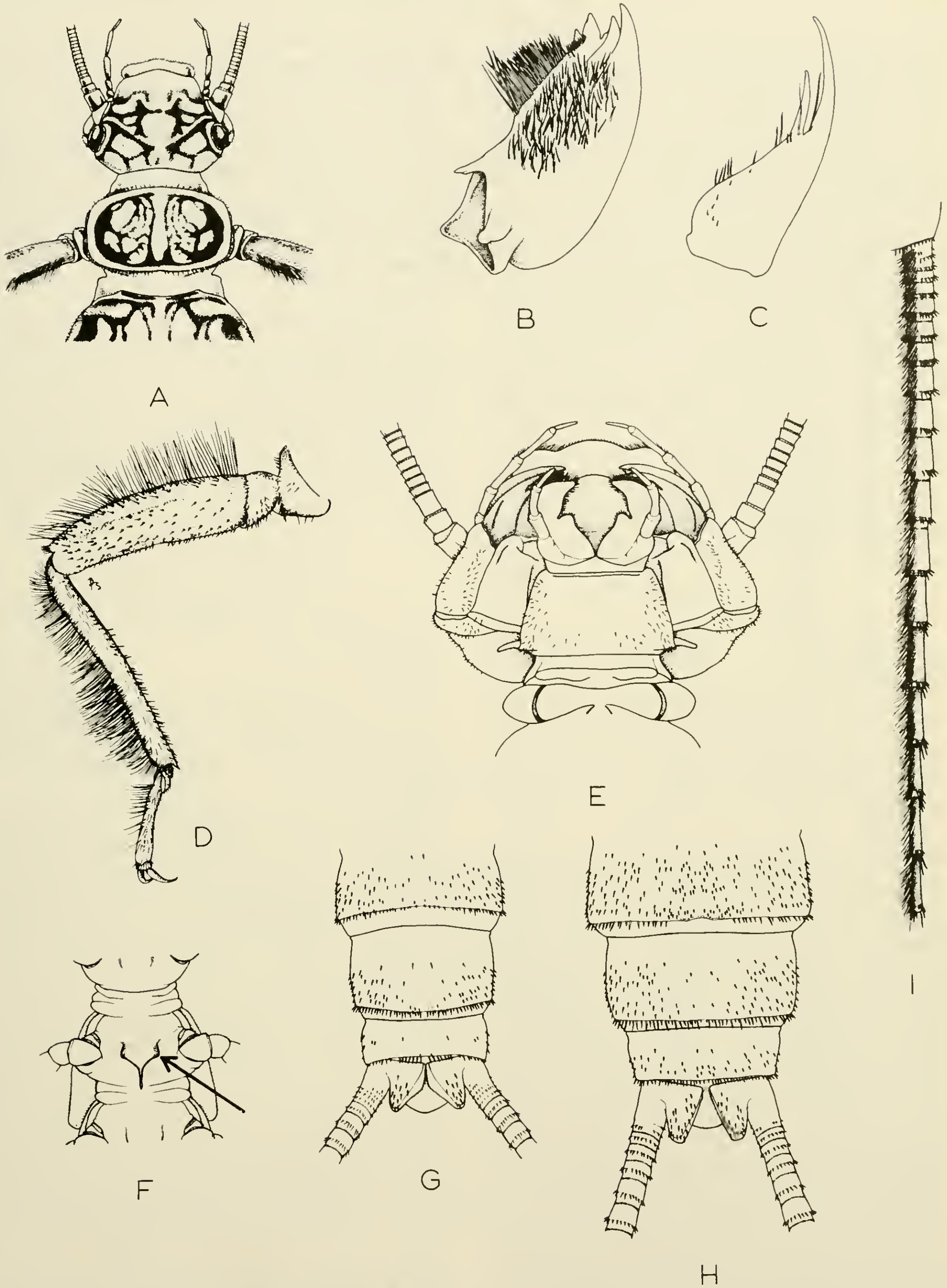

Fig. 17. Nymphal characters of *Pictetiella expansa*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, basal right cercal segments (dorsal).

fringe of golden, silky hairs (Fig. 17 D). Abdominal terga brown, with more than 100 intercalary spinules, and well-developed posterior fringe of stout setae, longest ones mesally. Cercal segments with apical whorl of stout setae and dorsal fringe of golden, silky hairs; cerci bicolored, with basal segments yellow and apical segments dark brown (Fig. 17 I). Posterior setal row of male 8th abdominal sternum continuous (Fig. 17 G); female with interrupted posterior 8th setal row and slight indication of developing subgenital plate (Fig. 17 H).

Nymph biology.— Poorly known. Found in streams 9000–9700 ft elevation in Colorado (Dodds and Hisaw 1975, and unique among the Perlodinae in having a late summer to fall emergence (July–Oct.) (Baumann and Gaufin 1969, Baumann et al. 1977). We successfully reared several mature nymphs collected near Provo, Utah, 31 Jul. 1982 within a period of 3 weeks.

North American species list/distribution.— Monospecific genus; *P. expansa* — COL, ID, MONT, UT, WYO.

Remenus Ricker

Type species.— *Remenus bilobatus* (Needham & Claassen).

Previous nymph descriptions/illustrations.— Claassen (1931; labrum, mandible, maxilla, labium), Frison (1942; habitus, mandible, maxilla, labium). Ricker (1952), Hitchcock (1974).

Nymph description.— (Figs. 18 A–J). Small; mature nymph less than 10 mm; body yellowish brown with little discernible pattern. Head with very faint M-mark forward of anterior ocellus; no distinct row of occipital spinules; 2–4 erect, stiff postocular setae (Fig. 18 A). Laciniae unidentate, abruptly narrowed near base (Fig. 18 C). Left mandible not deeply cleft, without serrations of teeth or median ventral setal patch (Fig. 18 B). Gills absent. Pronotum with faint reticulate pattern; 10–14 long erect marginal setae on each side (Fig. 18 A). Y-arms of mesosternum reach posterior corners of furcal pits (Fig. 18 E). Meso-metanota with faint reticulate pattern and dark brown wingpads; 1–3 erect setae anterolaterally, and a few short marginal setae (Fig. 18 A). Femora with stout, long setae over surface, but lacking a silky hair fringe (Fig. 18 D); tibiae with 10 or fewer short dorsal intercalary setae, and row of setae along base of well-developed golden, silky hair fringe (Fig. 18 D). Abdominal terga light brown, with fewer than 20 intercalary setae and posterior fringe of setae of alternate lengths, longest about 0.5 length of tergum. Cercal segments with apical whorl of long setae, some longer than following segment; no dorsal cercal silky fringe (Figs. 18 F–J). Posterior setal row of both male and female 8th abdominal sternum interrupted mesally (Figs. 18 F, G), but mature male nymph with elongate terminal process (Fig. 18 F).

Nymph biology.— Unknown except emergence is in Jun. in Great Smoky Mt. National Park (Frison 1942) and in West Virginia (R. F. Kirchner collection).

North American species list/distribution.— Monospecific genus; *R. bilobatus* — CONN, DEL, GA, NC, NY, PA, SC, TN, VA, WV.

Rickera Jewett

Type species.— *Rickera sorpta* (Needham & Claassen).

Previous nymph descriptions/illustrations.— Jewett (1955; head-pronotum, maxilla, labium), Szczytko and Stewart (1984; habitus, mandibles, laciniae, mesosternum, cerci).

Nymph description.— (Figs. 19 A–J). Body light brown with brown markings; antennae, legs cerci light brown. Head with dark, broad, irregular U-shaped mark connecting ocelli; light oval interocellar spot; light area anterior to median ocellus, sometimes with faint posterolateral arms forming an M-pattern (Fig. 19 A). Laciniae triangular and unidentate, with 5–6 basal marginal spinules and 2–3 medially located marginal spinules (Fig. 19 B). Left mandible not deeply cleft, teeth without serrations, and no separated median ventral patch of setae; dense row of unsocketed acanthae below dorsal tooth (Fig. 19 C). Gills absent. Pronotum encircled with light margin, then narrow dark band and coarsely reticulate interior pattern; glabrous, without setae or spinules (Fig. 19 A). Y-arms of mesosternum meet posterior corners of furcal pits, and transverse suture connects anterior corners of furcal pits (Fig. 19 E). Mesometanota glabrous without hairs or spinules. Femora yellowish brown with darker dorsal spot in apical half; band of setae 3–4 wide at

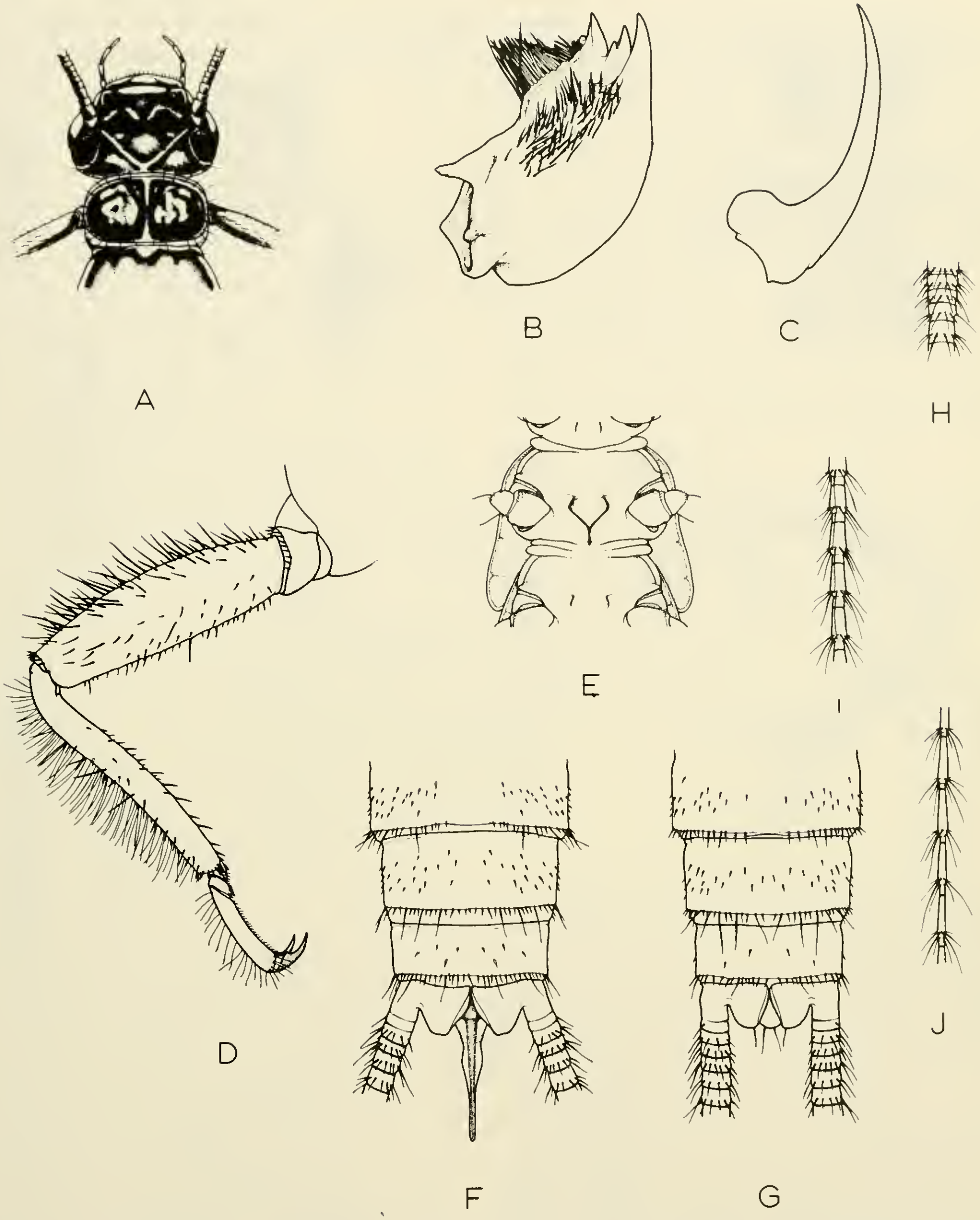

Fig. 18. Nymphal characters of *Remenus bilobatus*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen and terminalia; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

base of golden, silky hair fringe, and scattered over dorsal surface; tibial setal pattern similar to femora, and with golden, silky hair fringe (Fig. 19 D). Abdominal terga with light mesal spot margined by brown, giving abdomen the appearance of having a wide, light mesal band; segments 1–4 with fewer than 10 intercalary spinules and segments 5–10 with increasing number of intercalary spinules, up to 24–26. Cercal segments with apical whorl of stout setae and short dorsal fringe of golden, silky hairs (Figs. 19 H–J). Posterior setal row of male and female 8th abdominal sternae interrupted (Figs. 19 F, G); mesal posterior margin of female 8th sternum shallowly notched and sternae 8–10

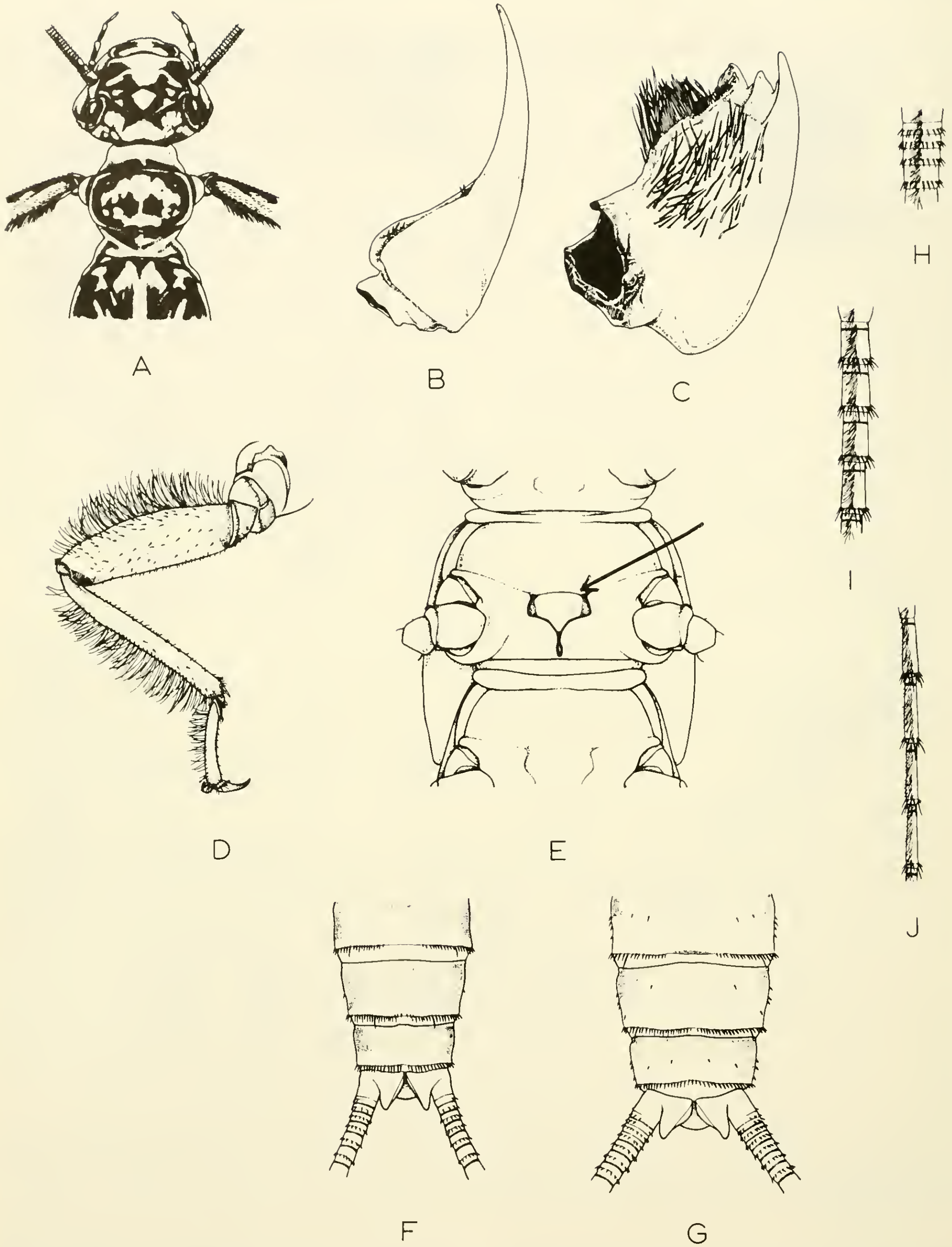

Fig. 19. Nymphal characters of *Rickera sorpta*: A, head, pronotum pattern; B, left lacinia (ventral); C, left mandible (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

with a few stout lateral intercalary spinules (Fig. 19 G).

NYMPH BIOLOGY.— Unknown, except that emergence occurs in early to mid-Jun. (Sheldon & Jewett 1967) to Jul. We reared adults from mature nymphs collected 6 Jul. 1979 in Hat Creek, Lassen Volcanic National Park, California.

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— Monospecific genus; *R. sorpta* —CAL, ORE, WN.

Setvena Illies

TYPE SPECIES.— *Setvena bradleyi* (Smith).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS.— (1) *S. tibialis* — Ricker (1952), Baumann et al. (1977). Nymphal characters have not been previously illustrated, except the gills (Shepard and Stewart 1983), (2) *S. bradleyi* — Claassen (1931; labrum, mandibles, maxilla, labium).

NYMPH DESCRIPTION.— (*S. bradleyi*) (Figs. 20 A–K). Body brown with dark brown pattern; dorsal surfaces with scattered small dark clothing hairs; antennae, legs, cerci brown. Frons, including interocellar area, brown, with faint lighter M-mark forward of anterior ocellus; occiput light brown with sinuate transverse row of stout spinules (Fig. 20 A). Lacinae triangular, bidentate with tuft of long setae on low knob below subapical tooth and continuous row of inner marginal setae, group of submarginal setae basally and 2 stout axillary setae; terminal tooth .035 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Fig. 20 B). Left mandible not deeply cleft, without serrations of teeth; median ventral patch of about 10 setae, and separate inner marginal patch of setae basally (Fig. 20 C). Short submental gills about 1.5–2.0 times as long as their basal diameter and fingerlike, simple gills anteroventrally on the meso- and metasternae (Fig. 20 F). Pronotum light brown with narrow, irregular, lighter mesal bar, lateral dark longitudinal bars and light interior reticulate markings; small spinules along front margin, absent along lateral and posterior margins (Fig. 20 A). Y-arms of mesosternum meet posterior corners of furcal pits and sinuate transverse furrow connecting anterior corners of furcal pits (Fig. 20 D). Meso- and metanota with a pair of light, central irregular round spots and other smaller light reticulate markings; transverse row of dark spinules across front ridge of wingpads; lateral marginal spinules small (Fig. 20 A). Femora brown with band of setae along base of golden, silky hair fringe and short setae and spinules along lower anterior surface; anterior (dorsal) surface covered with dark clothing hairs, except mesal band; tibiae covered with numerous stout intercalary setae and row of setae along base of golden, silky hair fringe (Fig. 20 E). Abdominal terga brown with >100 intercalary spinules; posterior fringe of setae on segments 1–7 restricted to mesal ⅓, but complete on segments 8–10, longest mesally. Cercal segments with apical whorl of short setae and dorsal fringe of golden, silky hairs (Figs. 20 I–K). Posterior setal row of male 8th abdominal sternum narrowly interrupted (Fig. 20 G); female 8th posterior setal row interrupted and posterior margin of 8th sternum with developing subgenital plate mesally (Fig. 20 H).

NYMPH BIOLOGY.— Unknown, except emergence of both species is during summer, Jun.–Aug. (Baumann et al. 1977, Jewett 1959). We reared one female *S. bradleyi* from a mature nymph collected 26 June 1981 in Teepee Creek, Lake Co., Montana.

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— (1) *S. bradleyi* — ALB, BC, ID, MONT, (2) *S. tibialis* (Banks) — BC, ORE, WN.

Skwala Ricker

TYPE SPECIES.— *Skwala parallela* (Frison).

PREVIOUS NYMPH DESCRIPTIONS/ILLUSTRATIONS. — (1) *S. curvata* — none, (2) *S. parallela* — Claassen (1931), Frison (1942; habitus, mandible, maxilla, labium), Ricker (1952), Baumann et al. (1977), Dosdall and Lehmkuhl (1979; left mandible, mesosternum), Shepard and Stewart (1983; gills).

NYMPH DESCRIPTION.— (*S. parallela*) (Figs. 21 A–K). Body yellowish brown with brown markings; sparse row of erect white, silky hairs behind ecdysial suture of head and as mesal row on thorax and abdomen; antennae, legs, cerci brown. Head dark with lighter M-mark forward of anterior ocellus and incomplete light mesal bar; 2 oval, light occipital spots inside eyes, broken with reticulate dark lines and bordered behind by narrow band of stout spinules (Fig. 21 A). Laciniae bidentate with tuft of setae on a low knob below subapical tooth and continuous inner row of marginal setae; complete band of submarginal setae; no separate median ventral patch of setae; terminal tooth about 0.4 total

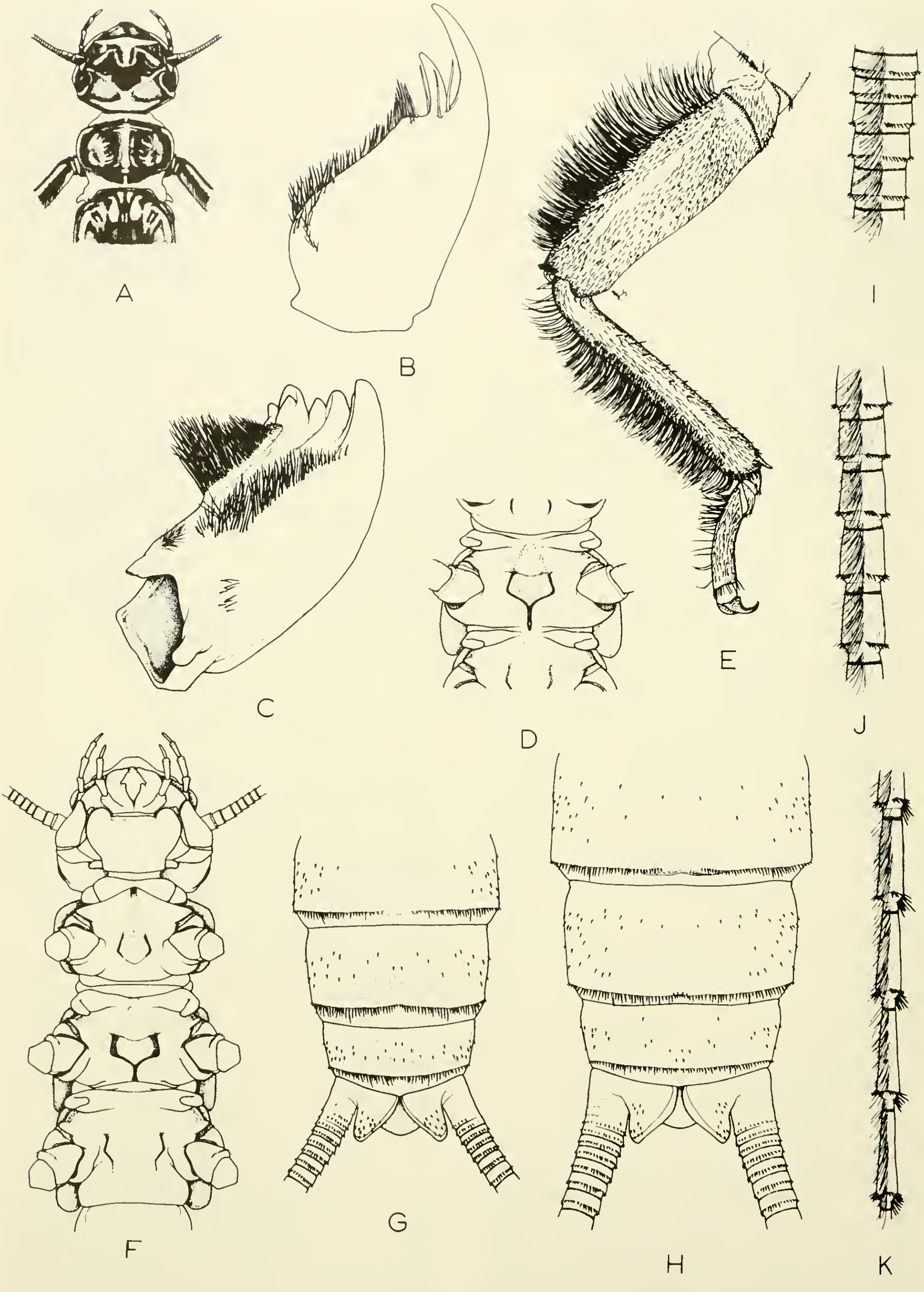

Fig. 20. Nymphal characters of *Setvena bradleyi*: A, head, pronotum pattern; B, left lacinia (ventral); C, left mandible (ventral); D, mesosternal Y-pattern; E, right front leg (anterior); F, submental and thoracic gills; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

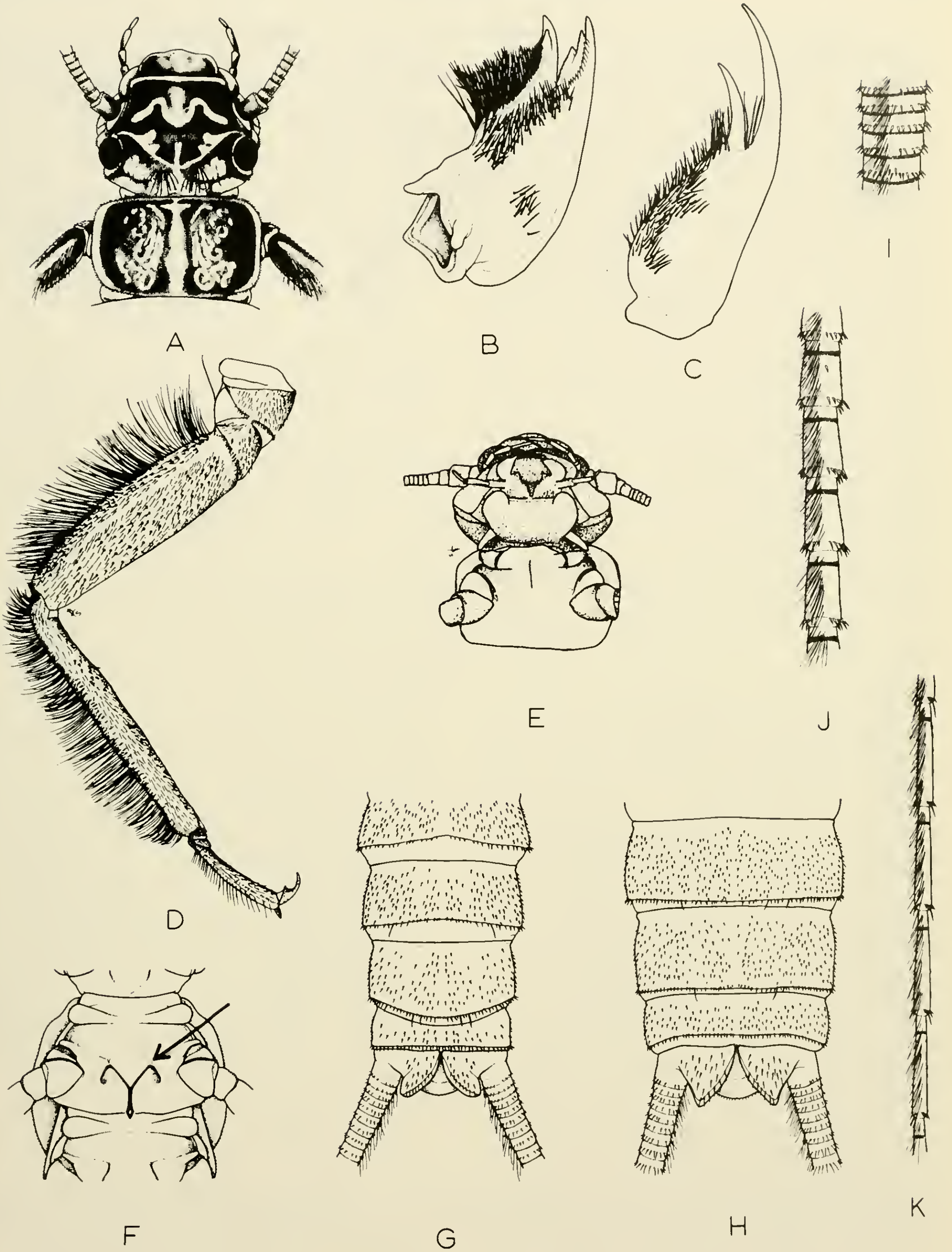

Fig. 21. Nymphal characters of *Skwala parallela*: A, head, pronotum pattern; B, left mandible (ventral); C, left lacinia (ventral); D, right front leg (anterior); E, submental gills; F, mesosternal Y-pattern; G, ♂ ventral abdomen; H, ♀ ventral abdomen; I, J, K, basal, middle, and apical cercal segments (dorsal).

outer lacinial length and subapical tooth about 0.6 length of terminal tooth (Fig. 21 C). Left mandible not deeply cleft; ventral teeth with well-developed serrations and median ventral patch of 12–14 setae present (Fig. 21 B). Long submental gills, projecting portion about 2.5–3.0 times as long as their basal diameter (Fig. 21 E). Pronotum dark with light lateral margins, light mesal band and light reticulate interior markings; complete row of short marginal spinules (Fig. 21 A). Y-arms of mesosternum reach anterior corners of furcal pits (Fig. 21 F). Meso- and metanota with irregular reticulate markings, darker areas with intercalary spinules; short setae across anteriormost transverse ridge of wingpads, continuous with lateral marginal setae. Legs brown, dorsal surfaces of femora and tibiae covered with short, stout setae, and both with golden, silky hair fringe (Fig. 21 D). Abdominal terga brown with mesal and lateral pairs of small light spots; densely covered with intercalary setae (>200) and margined posteriorly with a close-set row of short, stout setae. Cercal segments with apical whorl of short, stout setae and dorsal fringe of golden, silky hairs (Figs. 21 I–K). Posterior setal row of male 8th abdominal sternum more or less continuous (Fig. 21 G); female 8th setal row narrowly interrupted (Fig. 21 H).

Nymph biology.— Relatively well known for S. *parallela* and more generally for S. *curvata*. Univoltine in Colorado, with growth most rapid in late summer and fall; growth slows in winter but is continuous to Feb.–Apr., when emergence occurs (Short and Ward 1980). Young nymphs in Sep. in the Gunnison River, Colorado, were highly carnivorous, feeding predominantly on and showing positive electivity for Chironomidae larvae (Fuller and Stewart 1977). The diets of mature nymphs in early May were 75% animal matter, primarily mayfly and stonefly nymphs (Fuller and Stewart 1977). Richardson and Gaufin (1971) found that 41 fed guts of mature nymphs in Mar.–April contained 58.7% animal matter, primarily chironomids and mayfly nymphs, and 40.2% of a combination of detritus, filamentous green algae, and diatoms. The species is found primarily in foothill and lower-elevation rivers (Knight and Gaufin 1966, 1967, Ricker 1964), and generally emergence occurs Feb.–Jul., depending on altitude and latitude (Jewett 1959, Gaufin et al. 1972, Baumann et al. 1977, Short and Ward 1980). Sheldon (1972) found S. *curvata* to be the most abundant perlodid in Sagehen Creek. Small nymphs appear in late Jun. and display continuous growth until emergence from Apr. through early Jun. Nymphs fed on a variety of animal matter including Diptera, Ephemeroptera, Plecoptera, and Trichoptera.

North American species list/distribution.— (1) *Skwala curvata* (Hanson) — BC, ID, MONT, ORE, WN, WYO, (2) S. *parallela* — ARIZ, BC, CAL, COL, ID, MONT, NEV, NM, ORE, SASK, UT, WN, WYO.

Yugus Ricker

Type species.— *Yugus bulbosus* (Frison).

Previous nymph descriptions/illustrations.— (1) *Y. arinus* — Frison (1942; habitus, mandible, maxilla, labium, (2) *Y. bulbosus* — Frison (1942; habitus, mandibles, maxillae, labium), Ricker (1952), (3) *Y. innubilus* — none.

Nymph description.— (*Y. bulbosus*) (Figs. 22 A–J). Body yellow with light brown pattern; antennae, legs, cerci yellow. Head with light M-mark forward of anterior ocellus, bordered on front and rear with brown; interocellar area and area forward of ecdysial arms yellow; occiput with 2 light oval spots inside eyes, faintly broken by brown lines and partially bordered behind by an outer transverse band of spinules 2–4 wide (Fig. 22 A).Laciniae triangular, bidentate, with tuft of stout setae on low knob below subapical tooth and continuous inner row of stout marginal setae; 1 or 2 axillary setae and transverse band of setae across basal ventral surface; terminal tooth strongly curved, about 0.33 total outer lacinial length and subapical tooth about 0.5 length of terminal tooth (Figs. 22 C). Left mandible not deeply cleft, ventral teeth with barely discernible shallow serrations; no median ventral patch of setae (Fig. 22 B). Small nipplelike projection at posterior corners of submentum in some species we examined was suggestive of a very short or atrophied submental gill (also noted by Frison 1942); in other specimens submental gills were absent (also noted by Ricker 1952, Shepard and Stewart 1983). Pronotum encircled with narrow, light marginal band; mesal longitudinal light band and light reticulate interior markings; margined with short setae (Fig. 22 A). Y-arms of mesosternum meet posterior corners of furcal pits and

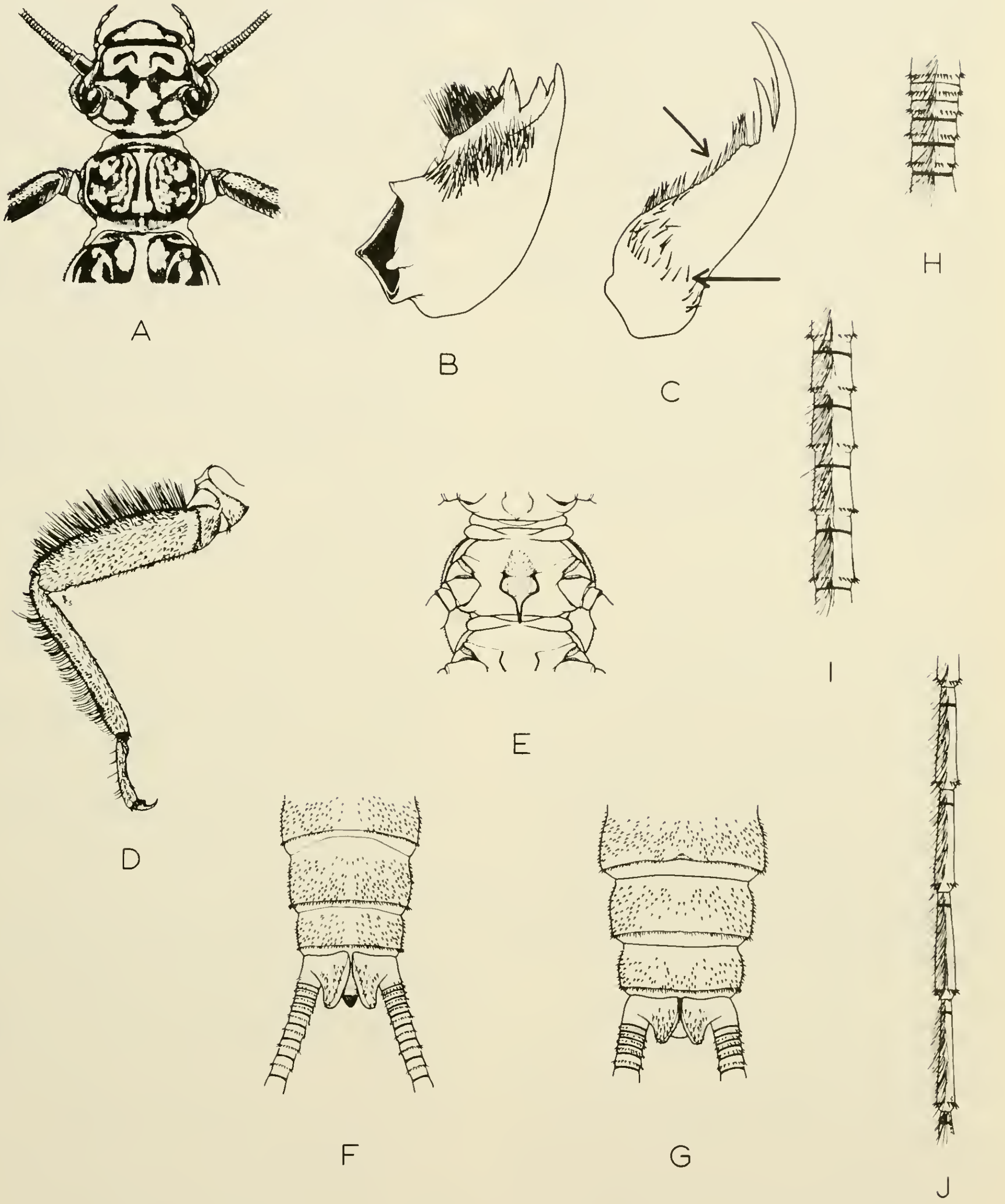

Fig. 22. Nymphal characters of *Yugus bulbosus*: A, head, pronotum pattern; B, left mandible (ventral); C, left maxilla (ventral); D, right front leg (anterior); E, mesosternal Y-pattern; F, ♂ ventral abdomen; G, ♀ ventral abdomen; H, I, J, basal, middle, and apical cercal segments (dorsal).

a faint incomplete transverse furrow is evident in some, with arms extending a short way inside anterior corners of furcal pits (Fig. 22 E).Meso-metanota with mesal light band and 2 round spots inside base of wingpads; transverse band of spinules along front ridge of wingpads and short lateral marginal spinules present (Fig. 22 A). Anterior femoral surface with short, stout intercalary setae and dark clothing hairs, except along mesal longitudinal bar; dorsal fringe of yellow, silky hairs; tibiae with hair pattern similar to femora (Fig. 22 D). Abdominal terga light brown except pair of yellow spots, giving the abdomen an appearance of having a central, broad, light longitudinal band; terga with >50 intercalary spinules and posterior row of short setae. Cercal segments with apical whorl of short setae and dorsal fringe of yellow, silky hairs (Figs. 22 H–J). Posterior setal row of male and female 8th abdominal sterna interrupted mesally (Figs. 22 F, G); female posterior margin of 8th sternum shallowly notched mesally at developing subgenital plate (Fig. 22 G).

NYMPH BIOLOGY.— Unknown, except emergence occurs Apr.–early Jun.

NORTH AMERICAN SPECIES LIST/DISTRIBUTION.— (1) *Yugus arinus* (Frison) — GA, NC, TN, VA, (2) *Y. bulbosus* — GA, NC, PA, SC, TN, VA, WV, (3) *Y. innubilus* (Needham & Claassen) — NC, TN

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LITERATURE CITED

ALLAN, J. D. 1982. Feeding habits and prey consumption of three Setipalpian stoneflies (Plecoptera) in a mountain stream. Ecology 63:26–34.

ASHLEY, D. L., D. C. TARTER, AND W. D. ATKINS. 1976. Life history and ecology of *Diploperla robusta* Stark & Gaufin (Plecoptera:Perlodidae). Psyche 83:310–318.

BAUMANN, R. W. 1973. Studies on Utah stoneflies (Plecoptera). Great Basin Nat. 33:91–108.

______. 1976. An annotated review of the systematics of North American stoneflies (Plecoptera). Perla 2:21–23.

BAUMANN, R. W., AND A. R. GAUFIN. 1969. The stoneflies of the Wasatch Mountains, Utah. Proc. Utah Acad. Sci. 46:106–113.

BAUMANN, R. W., A. R. GAUFIN, AND R. F. SURDICK. 1977. The stoneflies (Plecoptera) of the Rocky Mountains. Mem. Amer. Entomol. Soc. 31:1–208.

BRINCK, P. 1949. Studies on Swedish stoneflies. Opusc. Entomol. Suppl. 11:1–250.

______. 1952. Bäcksländor. Plecoptera-Svensk Insektfauna, Stockholm. 15:1–126.

CATHER, M. R., AND A. R. GAUFIN. 1975. Life history and ecology of *Megarcys signata* (Plecoptera:Perlodidae), Mill Creek, Wasatch Mts., Utah. Great Basin Nat. 35:39–48.

CLAASSEN, P. 1931. Plecoptera nymphs of America north of Mexico. Thomas Say Found. Ser. 31:1–199.

DESPAX, R. 1951. Faune de France, 55 Plécoptères:1–280. Paris, P. Lechevalier.

DODDS, G. S., AND F. L. HISAW. 1925. Ecological studies on aquatic insects IV. Altitudinal range and zonation of mayflies, stoneflies, and caddisflies in the Colorado Rockies. Ecology 6:380–390.

DONALD, D. B., AND R. S. ANDERSON. 1980. The lentic stoneflies (Plecoptera) from the Continental Divide region of Southwestern Canada. Can. Entomol. 112:753–758.

DOSDALL, L., AND D. M. LEMKUHL. 1979. Stoneflies (Plecoptera) of Saskatchewan. Quaest. Entomol. 15:3–116.

FRISON, T. H. 1935. The stoneflies, or Plecoptera, of Illinois. Bull. Ill. Natur. Hist. Surv. 20:281–471.

______. 1937. Studies of Nearctic aquatic insects. Bull. Ill. Natur. Hist. Surv. 2:89–90.

______. 1942. Studies of North American Plecoptera, with special reference to the fauna of Illinois. Bull. Ill. Natur. Hist. Surv. 22:299–301.

FULLER, R. L., AND K. W. STEWART. 1977. The food habits of stoneflies (Plecoptera) in the upper Gunnison River, Colorado. Environ. Entomol. 6:293–302.

______. 1979. Stonefly (Plecoptera) food habits and prey preference in the Dolores River, Colorado. Amer. Midl. Natur. 101:170–181.

GAUFIN, A. R. 1966. The stoneflies of Utah. Univ. Utah Biol. Ser. 14(1):1–93.

GAUFIN, A. R., W. E. RICKER, M. MINER, P. MILAM, AND R. A. HAYS. 1972. The stoneflies (Plecoptera) of Montana. Trans. Amer. Entomol. Soc. 98:1–161.

HARPER, P. P., AND J. G. PILON. 1975. Insectes aquatiques du nord du Québec (Ephémeroptères, Odonates, Plécoptères et Trichoptères). Ann. Soc. Entomol. Quebec 20:33–43.

HILSENHOFF, W. L. 1973. Perlodidae (Plecoptera) of Wisconsin. G. Lks. Entomol. 6:1–14.

HITCHCOCK, W. W. 1974. Guide to the insects of Connecticut. Bull. Conn. St. Geol. Natur. Hist. Surv. 107:1–262.

HYNES, H. B. N. 1941. The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. Trans. Roy. Entomol. Soc. London 91:459–557.

______. 1958. A key to the adults and nymphs of British stoneflies (Plecoptera). Freshw. Biol. Assn. Sci. Pub. 17:2–86.

ILLIES, J. 1955. Steinfliegen odor Plecoptera. Die Tierwelt Deutschlands und der angrezenden Meeresteile, Jena. 43:1–150.

JEWETT, S. G. 1955. Notes and descriptions concerning western North American stoneflies (Plecoptera). Wasmann J. Biol. 13:145–155.

_____. 1959. The stoneflies (Plecoptera) of the Pacific Northwest. Oregon State College Monogr. 3:76.

_____. 1960. The stoneflies (Plecoptera) of California. Bull. California Ins. Surv. 6:125–177.

_____. 1966. Notes on *Arcynopteryx (Oroperla) barbara* (Needham) (Plecoptera). Pan.-Pac. Entomol. 42:175–177.

Kerst, C. D., and N. H. Anderson. 1974. The Plecoptera community of a small stream in Oregon, USA. Freshw. Biol. 5:189–203.

Knight, A. W. 1965. Studies on the stoneflies (Plecoptera) of the Gunnison River drainage in Colorado. Unpublished dissertation. Univ. of Utah.

Knight, A. W., and A. R. Gaufin. 1966. Altitudinal distribution of stoneflies (Plecoptera) in a Rocky Mountain drainage system. J. Kansas Entomol. Soc. 39:668–675.

_____. 1967. Stream type selection and associations of stoneflies (Plecoptera) in a Colorado River drainage system. J. Kansas Entomol. Soc. 40:347–352.

Kondratieff, B. C., R. F. Kirchner, and J. R. Voshell, Jr. 1981. Nymphs of *Diploperla*. Ann. Entomol. Soc. Amer. 74:428–430.

Kondratieff, B. C., and J. R. Voshell. 1982. The Perlodinae of Virginia, USA (Plecoptera:Perlodidae). Proc. Entomol. Soc. Washington 84:761–774.

McCaskill, V. H., and R. Prins. 1968. Stoneflies (Plecoptera) of Northwestern South Carolina. J. Elisha Mitchell Sci. Soc. 84:448–453.

Minshall, G. W., and J. N. Minshall. 1966. Notes on the life history and ecology of *Isoperla clio* (Newman) and *Isogenus decisus* Walker (Plecoptera: Perlodidae). Amer. Midl. Natur. 76:340–350.

Needham, J. G. 1933. A stonefly nymph with paired lateral abdominal appendages. J. Entomol. Zool., Pomona College, Claremont (Cal.) 25:17–19.

Oberndorfer, R. Y., and K. W. Stewart. 1977. The life cycle of *Hydroperla crosbyi* (Plecoptera: Perlodidae). Great Basin Nat. 37:260–273.

Pekarsky, B. L. 1980. Predator-prey interractions between stoneflies and mayflies: behavioral observations. Ecology 61:932–943.

Pekarsky, B. L., and S. I. Dodson. 1980. Do stonefly predators influence benthic distributions in streams? Ecology 61:1275–1282.

Ray, D. H., and B. P. Stark. 1981. The Nearctic species of *Hydroperla* (Plecoptera:Perlodidae). Florida Entomol. 64:385–395.

Richardson, J. W., and A. R. Gaufin. 1971. Food habits of some western stonefly nymphs. Trans. Amer. Entomol. Soc. 97:91–121.

Ricker, W. E. 1943. Stoneflies of southwestern British Columbia. Indiana Univ. Publ. Sci. Ser. 12:1–145.

_____. 1952. Systematic studies in Plecoptera. Indiana Univ. Publ. Sci. 18:1–200.

_____. 1955. A collection of stoneflies (Plecoptera) from the Northwest Territories, Canada. Entomol. News 66:255–256.

_____. 1959. Plecoptera. Pages 941–957 *in* W. T. Edmondson, ed., Freshwater biology. John Wiley & Sons, New York. 1248 pp.

_____. 1964. Distribution of Canadian stoneflies. Gew. und Abw. 34/35: 50–71.

Ricker, W. E., and G. G. E. Scudder. 1975. An annotated checklist of the Plecoptera(Insecta) of British Columbia. Syesis 8:333–348.

Ross, H. H., and T. H. Frison. 1937. Studies of nearctic aquatic insects. Bull. Illinois Natur. Hist. Surv. 21:83.

Saltveit, S. J. 1978. The small nymphs of *Diura nanseni* (Kempny) (Plecoptera) Entomol. Scand. 9:297–298.

Shapas, T. J., and W. L. Hilsenhoff. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera and Trichoptera. Great Lakes Entomol. 9:175–188.

Sheldon, A. L. 1972. Comparative ecology of *Arcynopteryx* and *Diura* (Plecoptera) in a California stream. Arch. Hydrobiol. 69:521–546.

Sheldon, A. L., and S. G. Jewett, Jr. 1967. Stonefly emergence in a Sierra Nevada stream. Pan.-Pac. Entomol. 43:1–8.

Shepard, W. D., and K. W. Stewart. 1983. A comparative study of nymphal gills in North American stonefly (Plecoptera) genera and a new proposed paradigm of Plecoptera gill evolution. Misc. Pubs. Entomol. Soc. Amer. 55:1–58.

Short, R. A., and J. V. Ward. 1980. Life cycle and production of *Skwala parallela* (Frison) (Plecoptera: Perlodidae) in a Colorado mountain stream. Hydrobiologia 69:273–275.

Siegfried, C. A., P. J. Sheeham, and A. W. Knight. 1977. The adults of *Oroperla barbara*. Pan.-Pac. Entomol. 53:126–128.

Stark, B. P., and A. R. Gaufin. 1974. The genus *Diploperla* (Plecoptera:Perlodidae). J. Kansas Entomol. Soc. 47:433–436.

Stark, B. P., and D. H. Ray. 1983. A revision of the genus *Helopicus* (Plecoptera:Perlodidae). Freshw. Invert. Biol. 2:16–27.

Stark, B. P., and K. W. Stewart. 1981. The nearctic genera of Peltoperlidae (Plecoptera). J. Kansas Entomol. Soc. 54:285–311.

_____. 1982a. *Oconoperla*, a new genus of North American Perlodinae (Plecoptera:Perlodidae). Proc. Entomol. Soc. Washington 84:746–752.

_____. 1982b. Notes on *Perlinodes aurea* (Plecoptera: Perlodidae). Ann. Entomol. Soc. Amer. 75:84–88.

Stark, B. P., and S. W. Szczytko. In press. Egg morphology and classification of Perlodinae (Plecoptera: Perlodidae). Ann. de Limnol.

Stark, B. P., T. A. Wolff, and A. R. Gaufin. 1975. New records of stoneflies (Plecoptera) from New Mexico. Great Basin Nat. 35:97–99.

Stewart, K. W., B. P. Stark, and T. G. Huggins. 1976. The stoneflies (Plecoptera) of Louisiana. Great Basin Nat. 36:365–384.

Szczytko, S. W., and K. W. Stewart. 1977. The stoneflies (Plecoptera) of Texas. Trans. Amer. Entomol. Soc. 103:327–378.

_____. 1979. The genus *Isoperla* (Plecoptera) of western North America: holomorphology and systematics, and a new stonefly genus *Cascadoperla*. Mem. Amer. Entomol. Soc. 32:1–120.

_____. 1981. Reevaluation of the genus *Clioperla*. Ann. Entomol. Soc. Amer. 74:563–569.

_____. In press. Descriptions of *Rickera* Jewett, *Calliperla* Banks and two new western nearctic *Isoperla* species (Plecoptera). Ann. Entomol. Soc. Amer.

Zwick, P. 1973. Insecta: Plecoptera. Phylogenetisches system und katalog. das Tierreich, 94. Walter de Gruyter and Co., Berlin. 465 pp.

CHRYSOTHAMNUS NAUSEOSUS SSP. *UINTAHENSIS*: A STABILIZED HYBRID

Loran C. Anderson[1]

Abstract.— *Chrysothamnus nauseosus* ssp. *uintahensis* (Asteraceae) is formally described and illustrated. The new subspecies represents stabilized hybrids that most probably have *C. nauseosus* ssp. *hololeucus* x *C. parryi* ssp. *attenuatus* ancestry. Morphological and anatomical comparisons are made among the putatively related taxa.

While annotating the *Chrysothamnus* collection at Brigham Young University a few years ago, I encountered an unusual specimen from Uintah County (*Welsh & Moore 6759*). It looked intermediate between *C. nauseosus* and *C. parryi*, and I labeled it as "hybrid." Its pollen stainability was determined to be 60.4%. Later I received a collection from Sherel Goodrich that I thought was possibly a new subspecies of *C. nauseosus*. S. Goodrich, E. Neese, K. Thorne, and I observed the new subspecies in the field and made collections. Only after subsequent laboratory studies did I realize that the new subspecies and the Welsh collection were one and the same. *Chrysothamnus nauseosus* ssp. *uintahensis* appears to be a stabilized hybrid; it is technically described and illustrated (Fig. 1), and aspects of its biology are given.

Methods and Materials

Fresh materials of *Anderson 5513* and *5520* were processed for anatomical study as in Anderson (1970). Five heads were measured (as in Anderson 1964) for involucral and floral data. Cytological methods are those of Anderson (1966).

Taxonomy

Chrysothamnus nauseosus **(Pallas) Britt. ssp. *uintahensis* L. C. Anderson, ssp. nov.** Frutex humilis effusus plerumque 1–2 dm altus, caulibus decumbentibus vel ascendentibus tomentosis albis; folia linearia vel oblanceolata, 1–3 cm longa, 1–3 mm lata, cana vel viridia, in ramis floriferis superioribus plus minusve reducta; cyma paniculata compacta; capitula 11–13 mm longa, 2.2–2.7 mm lata, phyllariis 16–35 acuminatis vel cuspidatis subcarinatis basi margineque pilis sparsis obsitis; disci flosculi 4–5 flavi, tubis corollarum dilatatis plerumque 8–9.2 mm longis dense breveque pubescentibus, lobis 1–1.5 mm longis; lineae stigmaticae styli appendicibus saepissime breviores; achaenia dense pubescentia.

Type: Utah, Uintah Co., raw sandy clay of Duchesne River Formation, 2 mi ENE of Lapoint, 19 September 1981, *L. C. Anderson 5513* (Holotype: BRY; Isotypes: FSU, MO, NY, RSA, UC, UTC).

Low, spreading shrub 1–2(5) dm tall, stems white tomentose, decumbent or ascending; leaves grayish white or green, alternate, entire, linear to narrowly oblanceolate, 1–2(3) cm long, 1–2(3) mm wide, falcate, ascending, some weakly crispate, cuspidate, tomentose, more or less reduced on upper flowering branches; inflorescence a tightly congested paniculate cyme; heads (11)11.5–12.5(13) mm long, 2.2–2.7 mm wide, phyllaries (16) 18–32(35), stramineous, ovate to broadly lanceolate, weakly keeled in more or less vertical rows, sparsely pilose-tomentose basally or on margins, glabrous distally, acute to acuminate or cuspidate; disk flowers (4)5, yellow, corollas (7.2)8–9.2(9.7) mm long, tubes abruptly dilated at point of staminal departure (at ca 50% of total corolla length, Fig. 1e), densely short pubescent, lobes (0.9)1.0–1.5(1.8) mm long, lanceolate, erect; style 10.5–13.5 mm long, stigmatic lines usually much shorter than style appendages at 29–35%(52%) of style branch length; achenes

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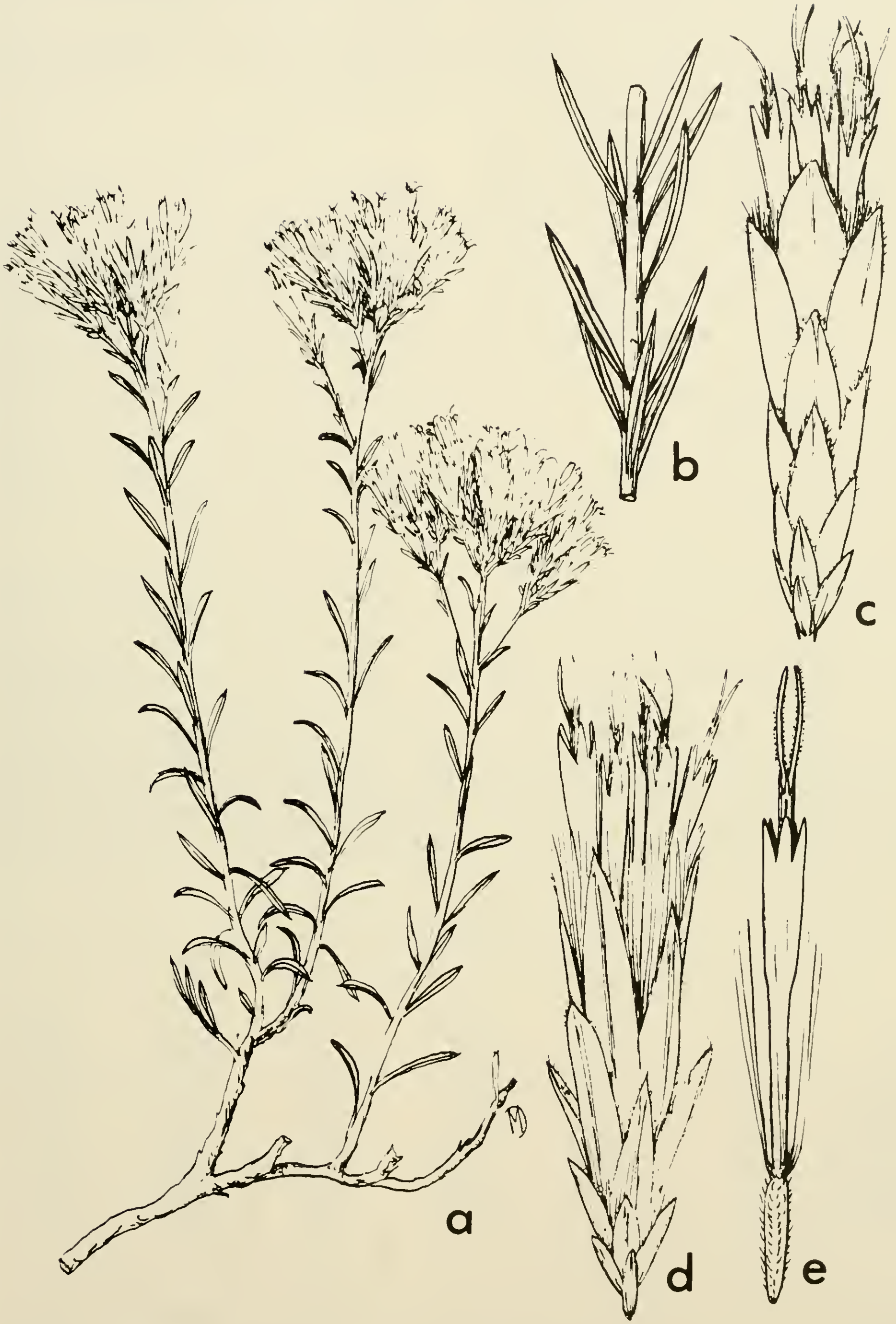

Fig. 1. *Chrysothamnus nauseosus* ssp. *uintahensis*: a, flowering branch (*Anderson 5513*); b, stem segment of *Anderson 5520* with larger leaves (same scale as a); c, flowering head of *Anderson 5520*, phyllaries acute and vertically aligned; d, flowering head of *Anderson 5513*, phyllaries acuminate, their vertical alignment less pronounced; e, flower with characteristic dilation of corolla tube.

cylindric, 6 mm long, densely villous, pappus 5.7–7.0 mm long; n = 9. Locally established on barren sandy clay or gypsiferous clay in open desert scrub (*Artemisia nova*, *Atriplex*, *Oryzopsis*, and *Stipa*), on Dakota Formation, Duchesne River Formation, or Mowry Shale, 5400–5750 ft, (July)September–October.

ADDITIONAL SPECIMENS EXAMINED.— Utah (all Uintah Co.): type locality, *L. C. Anderson 5516* (FSU, CS, DS, GH, NA, RM, UT), *5517* (BRY, FSU), S. *Goodrich 15263* (ASU, BRY, DS, FSU, MO, UTC), *19669* (BRY), *E. Neese et al. 11014* (BRY, FSU); 3.2 mi E of Lapoint, S. *Goodrich & R. Jepson 15944* (BRY, FSU); 0.4 mi E of Tridell, S. *Goodrich 19267* (BRY, FSU); 8 mi W of Maeser, S. *Goodrich 16427* (BRY, FSU); 4 mi W of Maeser, S. *L. Welsh & G. Moore 6759* (BRY, FSU, NY, UC); Steinaker Lake, *E. D. McArthur & A. C. Blauer 74-16* (SSLP), *74-17* (SSLP), both labeled as "*C. nauseosus* ssp. *salicifolius* x *C. parryi* ssp. *howardii*?"; Red Fleet Reservoir, 10.5 air mi NE of Vernal, *L. C. Anderson 5520* (BRY, FSU, MO, NY, UTC); *5521* (ASU, BRY, CS, COLO, FSU, MO, NA, NY, UT, UTC), *E. Neese & M. Chatterley 9892* (BRY, FSU); 15 mi E of Vernal, *E. Neese 6336* (BRY, FSU).

The new subspecies is striking in its rather barren setting with its yellow heads contrasted against green leaves and white stems. Its involucral bracts approach those of *C. parryi*, but the compact paniculate inflorescences are attributes of *C. nauseosus*. A collection from Cottonwood Creek Canyon in Emery County, *B. Maguire & B. L. Richards 14801* (UTC), may belong here or it may be anomalous; its final disposition has not been determined.

CYTOLOGY

The chromosome number in dividing root tip cells of *Anderson 5513* is 2n = 18. Meiotic material of *Goodrich 19669* was graciously supplied by S. Sanderson and E. D. McArthur. I was able to confirm their unpublished count of n = 9. Good bivalent formation occurs in meiosis. Meiotic regularity has been noted for other suspected hybrids (Anderson 1966, Anderson and Reveal 1966). Micronucleoli were prominent during latter stages of meiosis in some microsporocytes; they have been noted for other taxa in the genus (Anderson 1966, 1983).

Averages for pollen stainability in aniline blue in lacto-phenol are given for several collections in Table 1 in addition to the 60.4% reported for the Welsh collection. Several of the collections had irregular pollen grains such as unstained grains, dwarf and giant grains with stained protoplasts, and grains that were nonaperturate or polyaperturate. The mean pollen fertility for these populations of the Uintah Rabbitbrush is 76.7%, which is lower than that reported for the Ash

TABLE 1. Selected floral measurements for *Chrysothamnus nauseosus* ssp. *uintahensis* and related taxa.

		Involucre		
Collection (or taxon)	Pollen stainability	Bract number	Length mm	Width mm
Anderson 5513	.690	25.2	12.1	2.22
Anderson 5516	.975	26.4	11.7	2.22
Anderson 5520	.959	19.8	11.8	2.40
Anderson 5521	.662	17.6	11.6	2.34
Goodrich 15263	.960	32.4	12.4	2.69
Goodrich 19267	.822	16.6	11.6	2.40
Neese 9892	.461	28.8	12.2	2.76
MEANS				
C. nauseosus ssp. *uintahensis*	.767	23.8	11.9	2.43
C. nauseosus ssp. *hololeucus*		16.6	8.8	2.33
C. parryi ssp. *attenuatus*		14.0	13.4	3.19

Meadow hybrids (Anderson 1973) but higher than that of some interspecific hybrids in the genus (Anderson 1966). A direct correlation of pollen fertility to closeness of parental relationship cannot be made because of the high variance in pollen fertility among suspected hybrids in a given population or set of populations (Table 1 and Anderson 1973).

Floral Morphology and Anatomy

Measurements of selected floral features of the new subspecies are listed in Table 1, and means of the features for the subspecies and possibly related taxa are given. The Uintah Rabbitbrush is fairly uniform for involucral length but extremely variable for involucral bract number. Wide variance in that feature has been noted for a few other taxa (Anderson 1983). Another feature with considerable variability is the relative length of the stigmatic lines on the style branches; the stigmatic line:style branch ratio is usually reasonably constant for *Chrysothamnus* taxa (Anderson 1964). Variability in the Uintah Rabbitbrush may relate to its purported hybrid background.

Flowers have 5–7 (usually 5) vascular bundles in the ovary wall. The extra 1–2 bundles, when present, end blindly at the top of the achene rather than entering the corolla tube. Two style traces are present as is standard for the genus. Additional traces of phloem are directed toward the style base but terminate at the top of the ovary; that condition is found fairly frequently in *C. parryi* (Anderson 1970). Secretory canals are not as frequent in the flowers as they are in most *C. nauseosus* and *C. parryi*. They are fairly well developed in the achene, less so in the corolla, and absent in the style. Trichomes are abundant at two sites on the flower. The twin hairs of the achene average 470 μm long. The biseriate glandular hairs on the corolla tube usually have 12 cells and average 166 μm long. Trichomes are more abundant on the corolla tubes of the Uintah Rabbitbrush than in any other *Chrysothamnus*.

Relationships

Gross morphology justifies placing the new subspecies in *C. nauseosus*, but morphology of the involucre plus certain anatomical features strongly suggest that *C. parryi* is involved with its parentage. The most likely ancestral parents are *C. nauseosus* spp. *hololeucus* and *C. parryi* ssp. *attenuatus*. The Uintah Rabbitbrush has floral morphology that is largely intermediate to those two, i.e., involucral length and width (Table 1), phyllary shape and alignment (Fig. 1), involucral pubescence, corolla lobe length, and stigmatic line-style branch length ratio. The new subspecies is distinctive in its increased phyllary number and reduced corolla length.

Table 1 continued.

Disk flower						
Flower number	Corolla length mm	Corolla lobe length mm	Style length mm	Style branch mm	Stigmatic line: Style branch	Pappus mm
5.0	8.04	1.02	11.2	3.77	.296	6.24
5.0	7.97	0.91	12.8	3.74	.494	6.80
4.6	9.50	1.68	13.0	3.58	.326	6.14
5.0	8.31	1.05	13.3	3.62	.324	7.02
4.8	8.30	1.10	10.6	4.70	.521	6.23
5.0	8.74	1.22	11.0	4.02	.290	6.96
4.6	8.06	1.01	11.1	3.34	.354	5.70
4.9	8.42	1.14	11.9	3.82	.372	6.44
5.0	8.98	0.90	12.8	2.86	.532	6.44
5.3	9.62	1.64	14.4	4.56	.339	9.31

Floral anatomy correlates well with other phylogenetic indicators in *Chrysothamnus* such as karyology, aspects of gross morphology, and environmental preferences. The index of specialization (on a scale of 10), as determined from floral vasculature and secretory canal abundance (Anderson and Fisher 1970), ranges from 7.3 to 7.9 for *C. nauseosus* ssp. *uintahensis*. Indices for *C. nauseosus* ssp. *hololeucus* and *C. parryi* ssp. *attenuatus* are 5.4–5.6 and 5.2–5.6, respectively. Interestingly, the suggested level of specialization for the new subspecies (definitely derived) is higher than that of the parental groups even though one might expect its floral anatomy to be intermediate to that of the parents.

Uintah County is the northeastern boundary of the ranges for both suspected parental taxa. Actually, all interspecific hybridizations in *Chrysothamnus* occur at the edge of the range of at least one of the parental species even though the two parental taxa may be largely sympatric. Apparently some breakdown of internal genetic barriers accompanies the general stressing that must occur in geographically peripheral populations (Anderson 1966).

The Uintah Rabbitbrush is well established in a specific ecological setting. Abundance and distinctive morphology qualify these stabilized hybrids for taxonomic recognition. Since no general conclusions about the most appropriate way to treat such populations taxonomically exist (Raven 1980), I choose to recognize them as a subspecies of *C. nauseosus* because the majority of their expressed characteristics show that affinity.

Acknowledgments

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Literature Cited

Anderson, L. C. 1964. Taxonomic notes on the *Chrysothamnus viscidiflorus* complex (Astereae, Compositae). Madroño 17:222–227.

______. 1966. Cytotaxonomic studies in *Chrysothamnus* (Astereae, Compositae). Amer. J. Bot. 53:204–212.

______. 1970. Floral anatomy of *Chrysothamnus* (Astereae, Compositae). Sida 3:466–503.

______. 1973. Unique *Chrysothamnus* hybridizations in Ash Meadows, Nevada. Bull. Torrey Bot. Club 100:171–177.

______. 1983. *Chrysothamnus eremobius* (Asteraceae): a new species from Nevada. Brittonia 35:23–27.

Anderson, L. C., and P. S. Fisher. 1970. Phylogenetic indicators from floral anatomy in *Chrysothamnus* (Astereae, Compositae). Phytomorph. 20:112–118.

Anderson, L. C., and J. L. Reveal. 1966. *Chrysothamnus bolanderi*, an intergeneric hybrid. Madroño 18:225–233.

Raven, P. H. 1980. Hybridization and the nature of species in higher plants. Canad. Bot. Assoc. Bull. Suppl. 13(1):3–10.

DIATOMS OF THE MIDDLE FORK OF THE SALMON RIVER DRAINAGE, WITH NOTES ON THEIR RELATIVE ABUNDANCE AND DISTRIBUTION

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Abstract.— A total of 145 species of diatoms was collected from 13 sites in the Middle Fork of the Salmon River drainage, Idaho, USA. *Achnanthes minutissima* was the prevalent species with an importance index of 19.25. Cluster analysis revealed 2 main site groupings, sites above the entrance of Loon Creek and sites below. The entrance of Loon Creek (6th order) increases the Middle Fork of the Salmon River to a 7th order stream. Shannon-Weiner diversity values were generally high.

We have been characterizing the algal flora of Intermountain western North America for the past several years. At present, we are characterizing the diatom floras of several important stream systems in this area to add information to a general diatom flora of the region (Squires et al. 1973, Lawson and Rushforth 1975, Benson and Rushforth 1975, Clark and Rushforth 1977, Ross and Rushforth 1980, Rushforth et al. 1981a, Johansen and Rushforth 1981, and Cushing et al. 1983). Our studies have also extended to standing waters and other unique environments (e.g., Evenson et al. 1981, Felix and Rushforth 1979, Rushforth et al. 1981b, St. Clair and Rushforth 1976, and others).

The purpose of this paper is to document the species of diatoms in the Middle Fork of the Salmon River in Idaho and several of its important tributaries (Marsh Creek, Indian Creek, East Fork of Indian Creek, Loon Creek, and Big Creek). We also determined distributional patterns within this system and performed several statistical analyses of abundance. Data also are given for one site on the main Salmon River, just below the confluence with the Middle Fork (see Fig. 1 for collection sites).

Methods

Field

Samples were collected between 23 July and 1 August 1978. Diatom collections were made by brushing rocks with a stiff-bristle brush and collecting the algae in plastic bags. All samples were sent to the Philadelphia Academy of Natural Sciences for identification and enumeration. At the academy permanent slides were prepared and 1000 valves were randomly identified and enumerated from each site.

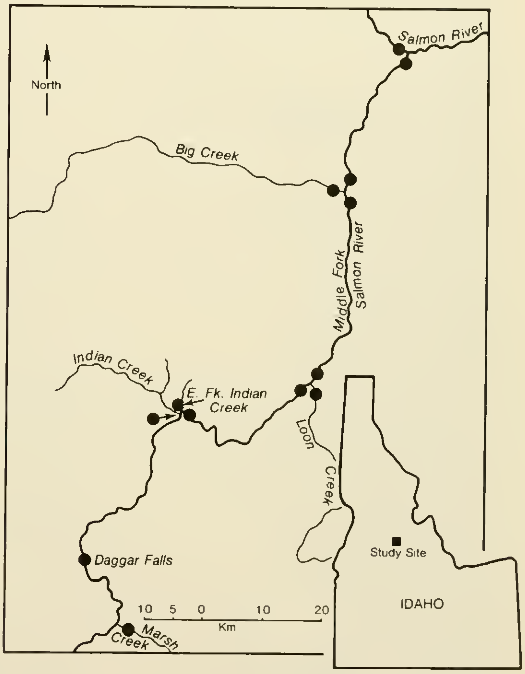

Fig. 1. Diagram of the Middle Fork of the Salmon River, Idaho, and its main tributaries. Black dots show sampling sites.

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These data were collected as part of a more extensive sampling regime intended to evaluate the influence of tributaries on certain ecological variables and predictions of the River Continuum Concept (Vannote et al. 1980). For a more complete description of the sampling sites and other data from these studies, see Bruns et al. (1982), Cushing et al. (1983), and Bruns et al. (1984).

Statistical Analyses

An "important species" index for diatom species encountered was calculated by multiplying the percent of a taxon in all samples (frequency of occurrence) by its average percent relative density in all samples (Ross and Rushforth 1980). This method is often used in studies of terrestrial vegetation (Warner and Harper 1972) and is advantageous since it considers both the frequency of occurrence of a species together with its percent relative density in each sample.

Similarity indices between the 13 samples collected were calculated following the methods of Ruzicka (1958). Calculated similarity indices were then clustered following Sneath and Sokal (1973) to examine if patterns of diatom distribution were evident. Diatom community diversity was measured for each sample using the Shannon-Wiener diversity index (Shannon and Weaver 1949, Patten 1962).

RESULTS AND DISCUSSION

There were 145 species of diatoms identified from these samples (Table 1). Cushing et

TABLE 1. Diatom distribution and percent relative abundance in the Middle Fork of the Salmon River, Idaho, drainage.

	Location[a]												
Species	1	2	3	4	5	6	7	8	9	10	11	12	13
Achnanthes austriaca v. *helvetica* Hust.	–[b]	0.2	–	–	–	–	–	–	–	–	–	0.1	0.4
A. biporoma Hohn & Hellerm.	–	0.1	–	–	–	0.2	–	0.2	0.1	0.1	–	0.2	0.7
A. detha Hohn & Hellerm.	0.1	1.1	–	0.1	–	0.3	–	–	0.5	0.3	–	1.0	–
A. didyma Hust.	–	–	–	–	–	–	–	0.1	–	–	–	–	–
A. exigua v. *heterovalva* Krasske	–	0.2	–	0.1	–	–	–	0.1	0.2	0.2	–	0.1	–
A. lanceolata (Bréb.) Grun.	5.6	3.3	18.1	5.5	3.1	5.1	0.7	1.3	14.7	3.1	0.4	3.8	0.5
A. lanceolata v. *dubia* Grun.	0.1	0.2	–	0.3	0.2	0.4	–	–	–	0.3	–	0.6	–
A. laterostrata Hust.	–	0.7	–	–	–	0.2	–	–	–	0.1	–	0.3	–
A. lewisiana Patr.	–	0.6	–	–	0.5	1.6	–	0.1	0.3	0.8	–	1.7	0.1
A. linearis (W. Sm.) Grun.	–	–	–	–	–	–	–	–	–	–	–	–	0.2
A. linearis v. *pusilla* Grun.	–	0.1	–	–	–	–	–	–	–	1.7	0.2	0.1	0.3
A. marginulata Grun.	0.1	0.1	–	–	–	–	–	–	0.4	–	–	–	0.1
A. minutissima Kütz.	31.5	11.5	5.2	41.2	9.6	29.2	0.5	20.4	27.1	62.6	14.9	16.2	16.3
A. peragalli Brun & Herib.	–	0.3	–	–	–	–	–	0.1	–	0.1	–	–	–
A. peragalli v. *parvula* (Patr.) Reim.	–	0.2	–	–	–	–	–	–	–	–	–	–	–
A. pinnata Hust.	–	–	–	–	–	–	–	0.1	–	–	0.1	–	0.1
Amphora ovalis v. *pediculus* (Kütz.) V.H. ex DeT.	0.5	0.6	–	0.2	0.1	–	–	0.2	–	0.2	0.4	–	–
A. perpusilla (Grun.) Grun.	0.3	0.2	–	0.3	0.2	0.7	0.1	0.4	0.1	–	1.0	0.1	0.1
Caloneis bacillum (Grun.) Cl.	–	–	–	–	–	–	–	–	–	–	–	–	0.1
Cocconeis diminuta Pant.	0.1	–	–	–	–	–	–	–	–	–	–	–	–
C. pediculus Ehr.	0.1	–	–	–	–	–	–	0.1	–	–	0.5	–	–
C. placentula Ehr.	–	–	0.2	0.2	0.1	0.1	–	–	–	–	–	–	–
C. placentula v. *euglypta* (Ehr.) Cl.	4.5	4.7	6.5	1.6	5.0	12.2	2.2	8.3	2.8	3.2	2.8	2.1	0.1
C. placentula v. *lineata* (Ehr.) V.H.	2.3	7.6	16.0	0.7	9.5	3.0	1.4	2.2	1.7	1.4	0.2	1.8	0.7
C. thumensis A. Mayer	–	–	–	–	–	0.1	–	–	–	–	–	–	–
Cyclotella meneghiniana Kütz.	–	–	–	–	–	–	–	–	–	–	–	0.1	–
Cymbella affinis Kütz.	–	0.1	–	–	0.1	–	–	–	0.2	0.1	5.9	–	0.2
C. brehmii Hust.	–	–	–	–	–	–	–	7.6	0.1	0.1	0.2	–	–

[a] 1–Indian Creek
2–Middle Fork below Indian Creek
3–East Fork, Indian Creek
4–Loon Creek
5–Middle Fork above Loon Creek
6–Middle Fork below Loon Creek
7–Big Creek
8–Middle Fork above Big Creek
9–Middle Fork below Big Creek
10–Middle Fork above Salmon River
11–Salmon River below Middle Fork, Salmon River
12–Middle Fork at Daggar Falls
13–Marsh Creek

[b] Blank denotes absence

Table 1 continued.

	Location[a]												
Species	1	2	3	4	5	6	7	8	9	10	11	12	13
C. cymbiformis (Ag.) Ag.	2.3	–	0.1	0.7	–	–	–	0.5	0.5	0.3	–	0.1	0.1
C. microcephala Grun.	–	–	–	–	–	0.2	–	0.4	0.2	0.1	–	–	0.1
C. minuta Hilse ex Rabh.	2.8	2.2	2.8	3.1	0.6	3.0	0.2	1.2	1.5	2.3	0.7	1.1	5.1
C. minuta v. *latens* (Krasske) Reim.	–	0.2	–	–	–	–	–	–	–	0.1	–	0.2	0.8
C. minuta v. *silesiaca* (Bleisch ex Rabh.) Reim.	0.5	0.7	1.2	0.4	0.4	0.2	0.1	0.3	0.2	0.7	–	0.4	2.0
C. minuta muelleri Hust.	1.3	0.9	0.1	0.1	0.5	0.3	–	0.3	0.1	0.1	–	0.2	0.1
C. naviculiformis Auersw. ex Heib.	–	–	–	–	–	–	–	–	–	–	–	–	0.1
C. prostrata (Berk.) Cl.	–	–	–	–	–	–	–	–	–	0.1	–	–	–
C. sinuata Greg	2.0	1.5	0.2	3.0	0.3	1.6	0.1	0.8	1.6	2.2	0.8	1.2	0.5
Denticula elegans Kütz.	0.1	–	–	0.1	–	–	–	–	–	–	–	–	0.2
Diatoma tenue Ag.	–	–	–	0.3	–	–	–	–	–	–	–	–	0.1
D. vulgare Bory	–	–	–	1.2	–	–	–	0.3	–	0.5	1.2	0.1	0.1
D. vulgare v. *breve* Grun.	0.6	1.2	0.4	0.4	0.4	0.1	–	0.2	0.6	0.5	–	0.7	0.8
Diatomella balfouriana Grev.	–	–	–	–	–	–	–	–	0.1	–	–	–	0.1
Didymosphenia geminata (Lyngb.) M. Schmidt	–	–	–	–	–	–	–	–	–	–	–	–	0.1
Epithemia adnata (Kütz.) Breb.	0.4	0.4	–	–	1.5	–	–	7.9	0.1	0.3	–	0.3	–
E. sorex (Kütz.)	–	0.2	–	0.1	1.1	0.3	–	5.7	1.3	2.6	2.9	–	–
E. turgida (Ehr.) Kütz.	–	1.7	–	–	2.9	1.7	0.4	6.8	0.6	0.6	0.1	2.3	–
Eunotia pectinalis v. *minor* (Kütz.) Rabh.	0.1	–	–	–	–	–	–	–	–	–	–	0.1	–
E. rabenhorstii v. *monodon* Grun.	–	–	–	–	–	–	–	–	–	0.1	–	–	–
E. tenella (Grun.) Cl.	–	0.1	–	–	–	–	–	–	–	–	–	0.2	–
E. tridentula Ehr.	–	–	–	–	–	–	–	–	–	–	–	–	0.1
Fragilaria brevistriata Grun.	–	–	–	–	–	0.1	–	0.1	0.1	–	–	0.2	–
F. construens v. *exigua* (W. Sm.) Schulz	–	–	–	–	–	–	–	–	–	–	–	–	0.2
F. construens v. *pumila* Grun.	0.4	8.7	–	0.7	4.0	1.1	0.1	1.3	2.9	2.8	0.6	2.9	3.4
F. construens v. *subsalina* Hust.	–	2.7	–	–	0.3	0.5	–	–	0.8	1.1	–	2.1	1.3
F. construens v. *venter* (Ehr.) Grun.	–	0.4	–	–	–	–	–	–	0.5	0.2	–	0.7	0.1
F. intermedia Grun.	–	–	–	–	–	–	–	–	–	–	–	–	0.2
F. leptostauron (Ehr.) Hust.	0.1	1.2	0.1	0.3	0.6	0.5	–	0.8	0.2	0.7	0.5	0.7	1.2
F. pinnata Ehr.	1.7	10.5	–	0.8	6.1	3.8	0.7	1.6	4.2	3.8	1.9	10.2	7.2
F. pinnata v. *lancettula* (Schum.) Hust.	0.2	0.5	–	0.1	–	0.4	–	–	–	–	–	0.2	0.3
F. vaucheriae (Kütz.) Peters.	5.5	6.8	31.8	8.0	5.5	3.3	1.0	1.2	5.3	4.8	15.6	5.3	7.2
Gomphoneis eriense (Grun.) Skv. & Meyer	0.2	–	0.4	1.7	0.1	–	0.1	–	1.4	3.3	0.2	0.1	–
G. herculeana (Ehr.) Cl.	0.4	0.2	–	1.9	–	–	0.4	–	0.5	0.8	–	–	0.1
G. herculeana v. *robusta* (Grun.) Cl.	0.2	–	–	0.5	–	–	–	–	–	0.1	0.2	–	–
Gomphonema angustatum (Kütz.) Rabh.	–	–	0.4	–	–	–	–	–	–	–	–	0.2	0.1
G. brasiliensis Grun	0.2	0.9	–	0.3	–	1.9	–	2.7	0.1	0.1	–	0.4	–
G. clevei Fricke	4.2	4.6	4.1	3.1	4.2	4.6	0.7	3.2	2.8	2.7	6.1	5.4	1.7
G. intricatum Kütz.	0.3	4.5	1.9	0.2	0.8	5.0	1.0	2.9	1.1	1.2	3.5	1.8	0.4
G. olivaceum (Lyngb.) Kütz.	–	0.1	–	4.4	0.1	0.1	0.2	–	0.2	0.1	–	–	–
G. olivaceoides Hust	0.6	0.7	0.4	6.2	–	1.2	–	0.3	0.6	1.4	0.8	0.4	0.4
G. parvulum (Kütz.) Kütz.	0.5	–	0.9	0.3	–	0.1	–	0.1	–	0.1	0.1	0.1	–
G. subclavatum (Grun.) Grun.	0.1	0.1	0.2	0.5	–	0.5	–	0.3	–	0.2	–	–	0.1
Hannaea arcus (Ehr.) Patr.	3.1	0.3	1.0	5.9	0.4	0.6	0.1	0.4	0.7	0.6	0.3	2.5	4.3
Hantzschia amphioxys (Ehr.) Grun.	–	–	–	–	–	–	–	0.1	0.6	–	–	–	–
Melosira distans v. *alpigena* Grun.	–	0.6	–	–	–	0.2	–	–	0.1	–	–	0.4	3.4
M. italica (Ehr.) Kütz.	–	0.3	–	–	0.2	–	–	0.6	0.1	–	–	0.2	0.6
M. italica v. *tenuissima* (Grun.) O. Müll.	0.4	2.6	–	–	0.8	–	–	–	0.3	0.3	–	1.9	1.2
M. varians C. A. Ag.	–	–	–	–	–	0.1	–	–	–	–	–	–	–
Meridion circulare (Greg.) Ag.	0.4	0.1	0.3	–	–	–	–	0.1	0.1	–	–	0.3	0.3
Navicula anglica Ralfs	–	–	–	–	–	–	–	–	–	–	–	0.1	–
N. arvensis Hust.	0.2	–	–	–	–	–	–	0.1	–	–	–	–	–
N. bryophila Peters.	–	–	0.1	–	–	–	–	2.2	–	0.3	–	–	–
N. cincta (Ehr.) Ralfs	0.1	–	0.3	0.3	0.1	0.2	–	0.4	0.2	0.2	–	0.1	–
N. cocconeiformis Greg. ex Grev.	–	–	–	–	–	–	–	–	–	–	–	0.1	–
N. convergens Patr.	–	–	–	–	–	–	–	–	–	–	–	0.1	–
N. contenta v. *biceps* (Arn.) V. H.	–	–	–	–	–	0.1	–	–	0.1	–	–	–	–
N. cryptocephala Kütz.	–	–	–	–	–	0.1	–	–	–	0.4	–	0.2	0.1

Table 1 continued.

Species	Location[a]												
	1	2	3	4	5	6	7	8	9	10	11	12	13
N. cryptocephala v. *veneta* (Kütz.) Rabh.	1.2	0.6	2.6	0.2	1.0	1.9	0.2	2.0	0.7	0.2	2.7	0.7	0.1
N. digna Hust.	0.1	–	–	–	–	–	–	–	–	–	–	0.1	–
N. indifferens Hust.	0.2	–	–	–	–	–	–	–	–	–	–	0.1	–
N. mediopunctata Hust.	–	–	–	–	–	–	–	–	–	0.1	–	–	–
N. menisculus Schum.	0.5	–	0.1	0.1	0.1	–	0.2	0.2	0.3	–	0.1	0.1	–
N. minima Grun.	0.8	2.5	0.3	–	0.4	0.7	–	0.1	0.5	0.7	–	1.8	0.6
N. minuscula Grun.	–	–	–	–	–	0.2	–	0.1	–	–	–	–	–
N. mutica Kütz.	–	–	–	–	–	–	–	–	–	0.1	–	–	–
N. mutica v. *cohnii* (Hilse) Grun.	–	–	–	–	–	–	–	1.1	1.6	0.3	–	–	–
N. mutica v. *undulata* (Hilse) Grun.	–	–	–	–	–	–	–	0.2	–	–	–	–	–
N. ochridana Hust.	–	–	–	–	–	–	–	0.1	0.1	0.4	–	0.4	–
N. pelliculosa (Breb. ex Kütz.) Hilse	0.2	–	–	–	–	–	–	–	–	–	–	–	–
N. pseudoscutiformis Hust.	–	0.1	–	–	–	–	–	–	–	0.1	–	–	0.1
N. pupula Kütz.	–	–	–	–	–	–	–	–	–	0.1	0.2	–	–
N. pupula v. *capitata* Skv. & Meyer	–	–	–	–	–	–	–	–	–	–	–	0.1	–
N. pupula v. *rectangularis* (Greg.) Grun.	–	0.5	–	–	–	–	–	–	–	–	–	–	–
N. radiosa Kütz.	–	0.1	–	–	–	0.1	–	–	–	–	–	0.1	–
N. radiosa v. *tenella* (Breb. ex Kütz.) Grun.	0.3	0.2	0.2	0.4	0.1	0.9	–	0.6	0.2	1.0	1.7	0.4	–
N. rhynchocephala Kütz.	–	–	–	–	–	–	–	–	–	–	–	0.1	–
N. salinarum v. *intermedia* (Grun.) Cl.	0.4	–	–	–	0.1	–	–	–	–	0.3	0.1	–	–
N. schoenfeldii Hust.	0.3	0.2	–	–	0.1	0.1	–	0.3	0.1	–	0.1	0.4	–
N. secreta v. *apiculata* Patr.	0.2	0.1	–	–	–	–	–	–	–	–	0.1	–	–
N. seminulum Grun.	11.7	0.6	0.2	0.1	29.5	0.3	87.0	0.1	2.5	3.9	1.0	0.4	–
N. tantula Hust.	0.1	–	–	0.1	–	–	–	0.2	–	–	–	0.3	0.1
N. tripunctata (O.F. Müll.) Bory	–	–	0.1	0.1	0.2	0.9	–	0.9	0.1	0.4	0.1	–	–
N. viridula (Kütz.) emend V.H.	–	–	–	–	–	0.1	–	–	–	–	0.1	–	–
Nitzschia angusta (W.Sm.) Grun.	–	–	–	–	0.1	–	–	–	–	–	–	–	0.2
N. amphibia Grun.	–	0.1	–	–	–	–	–	–	0.1	0.1	–	0.2	–
N. bicata Hust.	0.2	0.1	–	0.1	–	–	–	0.1	–	–	–	–	0.2
N. confinis Hust.	0.3	–	–	–	–	–	–	–	–	–	–	–	–
N. dissipata (Kütz.) Grun.	–	0.3	–	–	0.2	–	–	0.1	0.2	0.4	1.0	0.1	–
N. dissipata v. *media* Hantz.	1.4	–	0.3	0.9	0.7	1.0	–	–	0.2	0.3	1.3	–	0.3
N. fonticola Grun.	0.1	–	–	–	–	–	–	0.1	0.1	0.4	–	–	0.2
N. frustulum Kütz.) Rabh.	0.4	0.7	0.7	0.5	0.3	0.6	0.1	1.0	1.8	0.7	1.2	1.3	0.1
N. frustulum v. *perminuta* Grun.	1.0	2.2	0.4	1.3	1.5	1.9	0.1	3.5	2.9	5.3	1.6	5.0	1.1
N. frustulum v. *subsalina* Hust.	0.2	0.1	–	–	–	0.1	–	–	–	0.1	–	0.1	–
N. gracilis Hantz.	–	–	–	–	–	0.1	–	–	–	–	–	–	–
N. kuetzingiana Hilse	0.3	–	–	0.1	–	–	–	–	–	0.1	3.7	0.8	0.2
N. recta Hantz.	0.1	–	–	–	–	0.1	–	–	–	–	–	–	–
N. romana Grun.	1.9	0.2	–	0.2	–	0.5	0.2	0.5	0.5	0.4	0.2	0.5	0.4
N. tropica Hust.	–	–	0.2	–	–	–	–	–	–	0.1	–	0.1	–
Pinnularia biceps Greg.	–	–	–	–	0.1	–	–	–	–	–	–	–	–
P. borealis Ehr.	–	–	–	–	–	–	–	0.3	1.3	0.2	0.1	0.1	0.1
P. mesolepta (Ehr.) W. Sm.	–	–	–	–	–	–	–	–	–	0.1	–	–	–
P. obscura Krasske	–	–	–	–	–	–	–	0.1	–	–	–	–	–
P. subcapitata Greg.	0.1	–	–	–	–	–	–	–	–	–	–	–	–
Rhoicosphenia curvata (Kütz.) Grun. ex Tabh.	0.8	0.1	1.3	0.6	0.5	3.6	0.1	3.0	0.7	0.2	17.1	0.1	0.1
Rhopalodia gibba (Ehr.) O. Müll.	–	0.1	–	–	–	–	–	–	–	–	–	–	–
R. gibberula (Ehr.) O. Müll.	–	–	–	–	–	–	–	0.1	0.1	–	–	0.1	–
Stauroneis anceps Ehr.	–	0.1	–	–	–	–	–	–	–	–	–	–	–
S. kriegeri Patr.	0.1	–	–	–	–	–	–	–	–	–	–	–	–
Synedra mazamaensis Sov.	0.2	1.4	–	–	–	0.4	0.9	0.2	1.4	2.9	3.5	0.2	–
S. *minuscula* Grun.	–	0.9	0.2	–	0.1	0.2	–	0.2	0.5	0.3	0.2	2.6	17.6
S. *rumpens* Kütz.	1.0	0.5	–	0.1	0.4	0.6	0.1	–	0.6	0.5	0.1	2.1	1.7
S. *rumpens* v. *familiaris* (Kütz.) Hust.	–	0.3	–	–	–	–	–	–	–	0.1	–	–	0.2
S. *rumpens* v. *fragilarioides* Grun.	–	–	–	–	–	–	–	0.1	–	–	–	–	–
S. *rumpens* v. *meneghiniana* Grun.	0.4	–	0.7	–	0.1	–	–	–	0.2	0.3	–	–	0.5
S. *ulna* (Nitz.) Ehr.	1.4	1.3	–	0.4	5.2	0.5	1.1	0.8	5.4	4.1	1.6	10.1	12.1
Tabellaria flocculosa (Roth) Kütz.	–	–	–	–	–	0.1	–	–	–	–	–	–	0.1

al. (1983) reviewed the general distribution of the dominant species and stated that the Middle Fork system is characterized by an *Achnanthes minutissima* Kütz.-*Fragilaria pinnata* Ehr.-*Navicula seminulum* Grun.-*Cocconeis placentula* Ehr. species complex. Their analysis did not include the samples from the East Fork of Indian Creek, nor were statistical methods used. Both have been included in the present analysis and alter the dominant species complex somewhat. *Achnanthes minutissima* (importance value = 19.25) is the prevalent diatom throughout the system in terms of both occurrence and numbers. *Navicula seminulum* (9.75), *Fragilaria vaucheriae* (Kütz.) Peters (7.79), *Achnanthes lanceolata* (Bréb.) Grun. (5.02), *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. (4.31), *Cocconeis placentula* var. *lineata* (Ehr.) V.H. (3.73), *Fragilaria pinnata* (3.73), *Gomphonema clevei* Fricke (3.65), and *Synedra ulna* (Nitz.) Ehr. (3.14) are the other dominant taxa in the Middle Fork system (Table 2). Although *Navicula seminulum* is found throughout the Middle Fork system, its relatively high importance value is related to its high abundance in Big Creek; this occurrence is also reflected in the Shannon-Weiner value of 1.1 at this site (Table 3). The above taxa are common components of stream systems both in Europe (Johansson 1980, Kaweka 1981) and North America (Lawson and Rushforth 1975, Ross and Rushforth 1980).

Table 2. Importance values (percent presence x average frequency) of the dominant diatom species collected from the Middle Fork of the Salmon River drainage, Idaho.

Achnanthes minutissima	19.25
Navicula seminulum	9.75
Fragilaria vaucheriae	7.79
Achnanthes lanceolata	5.02
Cocconeis placentula var. *euglypta*	4.31
Cocconeis placentula var. *lineata*	3.73
Fragilaria pinnata	3.73
Gomphonema clevei	3.65
Synedra ulna	3.14
Rhoicosphenia curvata	2.17
Nitzschia frustulum var. *perminuta*	2.14
Fragilaria construens var. *pumila*	2.05
Cymbella minuta	2.05
Gomphonema intricatum	1.89
Hannaea arcus	1.55
Synedra minuscula	1.35
Cymbella sinuata	1.22
Navicula cryptocephala var. *veneta*	1.08
Epithemia turgida	0.91
Gomphoneis herculeana var. *robusta*	0.85
Nitzschia frustulum	0.72
Epithemia sorex	0.67
Synedra mazamaensis	0.59
Cymbella minuta var. *silesiaca*	0.50
Synedra rumpens	0.50

Our cluster analysis produced two groups of sample locations (Fig. 2). Although the clustering was not tight, a general pattern was evident. The first group of sites (Middle Fork below Big Creek, Middle Fork above Salmon River, Middle Fork below Loon Creek, Indian Creek, Loon Creek, and Middle Fork above Big Creek), with the exception of Indian Creek, essentially make up the lower sections of the Middle Fork drainage below Loon Creek. The second group (Middle Fork below Indian Creek, Middle Fork at Daggar Falls, Marsh Creek, and Middle Fork above Loon Creek) constitutes the upper drainage basin section above Loon Creek. It is perhaps significant that the Middle Fork of the Salmon changes from 6th to 7th order where it receives 6th order Loon Creek. This results in a 33% increase in flow volume (J. T. Brock, pers. comm.) and a coincident increase in mean depth since the channel width does not change markedly at this location. Similarly, Bruns et al. (1982) reported that the largest portion of ecological change in the Middle Fork drainage system occurred upstream of the entrance of Loon Creek, and only slight changes occurred below. Bruns et al. (1982) were using link analysis, rather than stream order, and the site at Loon Creek was at link magnitude 1000. The final three sites were atypical of the rest and clustered with them at low values. These sites

Table 3. Shannon-Wiener diversity index values for 13 sites on the Middle Fork of the Salmon River drainage, Idaho.

Site	Diversity
Marsh Creek	4.2
Middle Fork at Daggar Falls	4.8
Indian Creek	4.2
Middle Fork below Indian Creek	4.8
East Fork, Indian Creek	3.3
Loon Creek	3.6
Middle Fork above Loon Creek	3.9
Middle Fork below Loon Creek	4.3
Big Creek	1.1
Middle Fork above Big Creek	4.6
Middle Fork below Big Creek	4.3
Middle Fork above Salmon River	4.7
Salmon River below Middle Fork, Salmon River	4.2

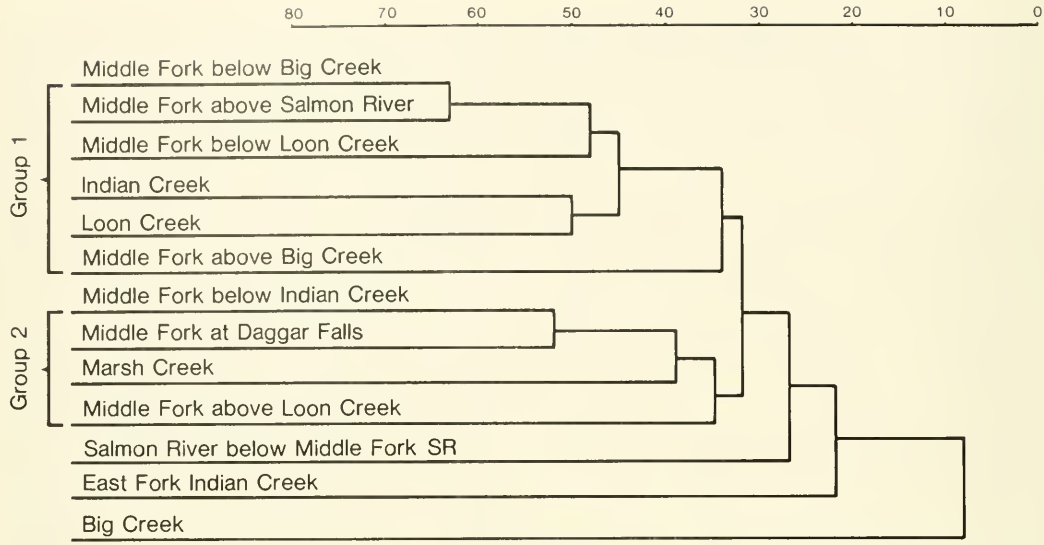

Fig. 2. Dendrogram showing results of cluster analysis of 13 sites on the Middle Fork of the Salmon River, Idaho, and its tributaries.

included the main Salmon River below the Middle Fork, the East Fork of Indian Creek, which is a small, heavily shaded 3rd order site, and Big Creek, which had high detritus standing crops (G. W. Minshall, pers. comm.) and low species diversity.

Calculated Shannon-Weiner diversity values are generaly quite high (Table 3). All values exceeded 3.3 with the exceptions of the East Fork of Indian Creek and Big Creek. Highest diversities were found in the Middle Fork below Indian Creek (4.8), in the Middle Fork at Daggar Falls (4.8), and at the mouth of the Middle Fork (4.7). No general pattern was evident in these data, with high and low values generally distributed throughout the system.

This study has presented data on the dominant diatoms in the Middle Fork of the Salmon River system. Future floristic and ecological studies in this region should enhance our initial species list and will further contribute knowledge of the diatoms of western North America.

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LITERATURE CITED

BENSON, C. E., AND S. R. RUSHFORTH. 1975. The algal flora of Huntington Canyon, Utah, USA. Bibliotheca Phycologica 18:1–177.

BRUNS, D. A., G. W. MINSHALL, J. T. BROCK, C. E. CUSHING, K. W. CUMMINS, AND R. L. VANNOTE. 1982. Ordination of functional groups and organic matter parameters from the Middle Fork of the Salmon River, Idaho. Freshw. Invertebr. Biol. 1(3):2–12.

BRUNS, D. A., G. W. MINSHALL, C. E. CUSHING, K. W. CUMMINS, J. T. BROCK, AND R. L. VANNOTE. 1984. Tributaries as modifiers of the river continuum concept: analysis by polar ordination and regression models. Arch. Hydrobiol. 99:208–220.

CLARK, R. L., AND S. R. RUSHFORTH. 1977. Diatom phytoplankton and periphyton studies of the headwaters of Henry's Fork of the Snake River, Island Park, Idaho, USA. Bibliotheca Phycologica 33:1–204.

CUSHING, C. E., K. W. CUMMINS, G. W. MINSHALL, AND R. L. VANNOTE. 1983. Periphyton, chlorophyll *a*, and diatoms of the Middle Fork of the Salmon River. Holarc. Ecol. 6:221–227.

EVENSON, W. E., S. R. RUSHFORTH, J. D. BROTHERSON, AND N. FUNGLADDA. 1981. The effects of selected physical and chemical factors on attached diatom populations in the Uintah Basin of Utah, USA. Hydrobiologia 83:325–330.

Felix, E. A., and S. R. Rushforth. 1979. The algal flora of the Great Salt Lake, Utah, USA. Nova Hedwigia 31:163–195.

Johansen, J. R., and S. R. Rushforth. 1981. Algae of surface waters and soils of the federal oil shale lease areas of eastern Utah. Nova Hedwigia 34:333–390.

Johansson, C. 1980. Attached algal vegetation in two stony streams in NW Jamtland, Sweden. Ecology, volume and primary production. Medd. Vaxtbiol. inst., Uppsala 1, 15 pp. + append.

Kawecka, B. 1981. Sessile algae in European mountain streams. 2. Taxonomy and autecology. Acta. Hydrobiol. 23:17–46.

Lawson, L. L., and S. R. Rushforth. 1975. The diatoms of the Provo River, Utah. Bibliotheca Phycologica 17:1–149.

Patten, B. C. 1962. Species diversity in net phytoplankton of Raritan Bay. J. Marine Res. 20:57–75.

Ross, L. E., and S. R. Rushforth. 1980. The effects of a new reservoir on the attached diatom communities in Huntington Creek, Utah. Hydrobiologia 68:157–165.

Rushforth, S. R., J. D. Brotherson, N. Fungladda, and W. E. Evenson. 1981a. The effects of dissolved heavy metals on attached diatoms in the Uintah Basin of Utah, USA. Hydrobiologia 83:313–323.

Rushforth, S. R., L. L. St. Clair, J. Grimes, and M. C. Whiting. 1981b. The phytoplankton of Utah Lake. Great Basin Nat. Mem. 5:85–100.

Ruzicka, M. 1958. Anwendung mathematisch-statistischer Methoden in der Geobotanik (Synthetische Bearbeitung von Aufnahmen). Biologia, Batisl. 13:647–661.

Shannon, C. E., and W. Weaver. 1949. The mathematical theory of communication. Univ. of Illinois Press, Urbana. 117 pp.

Sneath, P H. A., and R. R. Sokal. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco. 573 pp.

Squires, L. E., S. R. Rushforth, and C. J. Endsley. 1973. An ecological survey of the algae of Huntington Canyon, Utah. BYU Sci. Bull., Biol. Ser. 18(2):1–87.

St. Clair, L. L., and S. R. Rushforth. 1976. The diatom flora of Timpanogos Cave National Monument, Utah. Amer. J. Bot. 63:49–59.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37:130–137.

Warner, J. H., and K. T. Harper. 1972. Understory characteristics related to site quality for aspen in Utah. BYU Sci. Bull., Biol. Ser. 16(2):1–20.

NOTES ON THE WHITE-TAILED ANTELOPE SQUIRREL, *AMMOSPERMOPHILUS LEUCURUS*, AND THE PINYON MOUSE, *PEROMYSCUS TRUEI*, IN NORTH CENTRAL NEVADA

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ABSTRACT.— A four-season live trapping study in the Whirlwind Valley, on the Lander and Eureka county lines near the Humboldt River, yielded two species previously unrecorded from both counties, *Ammospermophilus leucurus* and *Peromyscus truei*. Both records represent minimal airline range extension of 113 and 105 km. It is suggested that the distribution of *A. leucurus* may include the entire northeastern quadrant of Nevada. The occurrence of *P. truei* in sagebrush habitat 21 km from the nearest pinyon woodland is unusual and suggests that this species may occur patchily distributed throughout the lower elevation ranges in the northern portion of the state.

A recent baseline inventory study in the Whirlwind Valley, Lander and Eureka counties, Nevada, furnished several noteworthy observations of small mammals. A substantial range extension for the white-tailed antelope squirrel (*Ammospermophilus leucurus*) was documented. Also, a range extension and an unusual habitat occurrence was found for the pinyon mouse (*Peromyscus truei*).

Seasonal data were obtained on five trapping plots that sampled representative habitat types for the area. Four plant associations (Cronquist et al. 1972) occurred within the study area: Shadscale Association dominated by shadscale (*Atriplex confertifolia*), budsage (*Artemisia spinescens*), peppergrass (*Lepidium perfoliatum*), and small star (*Microsteris gracilis*); Big Sagebrush Association dominated by big sagebrush (*Artemisia tridentata*), Nevada bluegrass (*Poa nevadensis*), snakeweed (*Gutierrezia sarothrae*), and small star; Greasewood Association dominated by greasewood (*Sarcobatus vermiculatus*), inkweed (*Suaeda fruticosa*), and smallscale (*Atriplex pusilla*); Marsh-Meadow Association dominated by saltgrass (*Distichlis stricta*), wire rush (*Juncus balticus*), and sedge (*Carex* sp.).

Plot 1 (T31N, R47E, Sec. 24 NW¼ of SW¼) was placed to sample a combination of Shadscale and Big Sagebrush associations and was situated at the base of the Malpais escarpment. Plot 2 (T31N, R47E, Sec. 13 SW¼ of SE¼) sampled a relatively homogeneous area of Shadscale Association. Plot 3 (T31N, R48E, Sec. 18 NW¼ of NE¼) was placed in homogeneous Marsh-Meadow Association. Plot 4 (T31N, R48E, Sec. 4 SE¼ of SE¼) was placed in relatively homogeneous Greasewood Association. These plots were on the valley floor, whereas Plot 5 (T31N, R48E, Sec. 20 SW¼ of SW¼) was placed in homogeneous Big Sagebrush Association on the Malpais escarpment, approximately 152 m elevation above the valley floor.

Trapping, using standard Sherman live traps, was conducted for six consecutive nights each in May, July, and September 1982 and January 1983 during the new moon phase. Each trapping plot consisted of two parallel lines transected by four assessment lines (modified from O'Farrell et al. 1977) covering an area of about 22 ha.

The July, September, and January sampling periods yielded multiple captures of *A. leucurus* on Plots 1, 2, and 5. On Plot 1 two adult individuals of each sex were captured in July and September. They occurred only in the big sagebrush component of the habitat, associated with a wash; mean vegetation height was 90.0 cm and cover was 35.0%. Plot 2 yielded three adults, two males and one female, in July, September, and January. Most captures occurred in relatively pure shadscale; mean vegetation height was 19.4 cm and cover was 17.8%. On Plot 5, only one adult male was captured in July; mean vegetation height was 40.6 cm and cover was 28.7%.

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From many years of personal observation in southern Nevada, one of us (M.J.O'F.) has noted that *A. leucurus* is commonly seen during the crepuscular hours, particularly along roadways. Also, during the spring and summer months, the species is quite evident by characteristic "trilling" vocalizations. However, in the Whirlwind Valley no vocalizations were heard and only a few individuals were observed running around the rocky hillsides at the base of the Malpais escarpment in July and September. No others were observed, except in traps, throughout the rest of the valley.

Hall (1981) provides the most recent examination of the distribution of *A. leucurus* over its entire range. The distribution in Nevada excludes the north central and most of the northeastern portion of the state. The Whirlwind Valley location represents an airline range extension of about 113 km (70 mi) from the nearest recorded location at the S base of Granite Peak, east range, Pershing County; three mountain ranges lie between these two locations. The remaining known locations occur in a nearly complete circle around the Whirlwind Valley location at distances not exceeding 274 km (170 mi). We suggest that systematic sampling throughout the northeastern portion of Nevada may reveal the presence of *A. leucurus*, justifying a major modification of present range maps.

During the last half of the study, we obtained captures of *P. truei* on Plots 1 and 5. An adult male was captured only once on Plot 1 in September; the point of capture was in homogeneous Shadscale Association. Four adults, two of each sex, were captured on Plot 5 during September and January. A female captured in September was in a postlactating condition. All individuals were caught in homogeneous Big Sagebrush Association with rocky substrate.

The most recent projected range map for *P. truei* (Hall 1981) indicates that the Whirlwind Valley is at the estimated edge of the range. However, a more detailed examination of the known distribution in Nevada (Hall 1946), using the same locations as the more recent work, show the nearest location to the Whirlwind Valley as the W side of Ruby Lake, about 105 km (65 mi) distant. Also, there are no records of *P. truei* in either Lander or Eureka counties.

The occurrence of *P. truei* in pure stands of either Big Sagebrush or Shadscale associations is unusual considering that the nearest pinyon habitat is over 21 km (13 mi) away from the sampling locations. Hall (1946) reported this species restricted to pinyon woodland with rocky substrate. Douglas (1969) found that *P. truei* was not resident in brush areas that lacked pinyon logs, although the mouse would venture into adjacent habitat to occasionally forage. He further noted that rocky substrate was not required; however, populations tended to be higher in such areas due to use of rocks as subsidiary nesting areas.

Although the capture on Plot 1 was obviously a transient individual, the presence and increase in numbers over a two-season period on Plot 5 indicates a resident status. Inasmuch as the nearest pinyon woodland is far removed, we surmise that *P. truei* is patchily distributed throughout the Big Sagebrush Association in the Shoshone Range, of which the Malpais escarpment is a projection. This may be the case for many of the lower mountain ranges in central and northern Nevada. Such scattered populations may fluctuate greatly depending on available resources and reproductive success in optimal habitat. They may also serve to maintain the genetic integrity of the species. Further work with these populations is certainly warranted.

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Literature Cited

Cronquist, A., A. Holmgren, N. Holmgren, and J. Reveal. 1972. Intermountain flora: vascular plants of the intermountain west, USA. Vol. 1. Hafner Publ. Co., Inc., New York. 270 pp.

Douglas, C. L. 1969. Comparative ecology of pinyon mice and deer mice in Mesa Verde National Park, Colorado, Univ. Kansas Publ. Mus. Nat. Hist. 18:421–504.

HALL, E. R. 1946. Mammals of Nevada. Univ. of California Press, Berkeley. 710 pp.

_____. 1981. The mammals of North America, 2d ed. John Wiley and Sons, New York. Vol. 1:1–600 + 90 pp. Vol. 2:601–1181 + 90 pp.

O'FARRELL, M. J., D. W. KAUFMAN, AND D. W. LUNDAHL. 1977. Use of live trapping with the assessment line method for density estimation. J. Mammal. 58:575–582.

GENETICS OF HYBRIDIZATION BETWEEN THE POCKET GOPHERS *THOMOMYS BOTTAE* AND *THOMOMYS TOWNSENDII* IN NORTHEASTERN CALIFORNIA

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Abstract.— Hybridization between the pocket gophers *Thomomys bottae* and *T. townsendii* at Gold Run Creek in Honey Lake Valley, Lassen County, California, is examined by electromorphic and morphologic characters and by the distribution of ectoparasitic mallophagan lice. Hybrid formation is minimal (about 12% of the total sample of 104 individuals examined), but both F_1 hybrids and a few presumptive backcross individuals are apparent. Nevertheless, no evidence of genic introgression based on five diagnostic allozyme loci is present in parental populations of either taxon within a mile of the hybrid zone. Similarly, louse species unique to each parental gopher host do not penetrate beyond the geographic limits of the genetic hybrid zone into the range of the opposite gopher species. A narrow zone of hybridization is thus concordantly defined by genetic, morphologic, and ectoparasitic parameters. These two gopher taxa are thus genetically if not reproductively isolated and should be considered separate biological species.

Thaeler (1968) was the first to record hybridization between the pocket gophers (*Thomomys bottae* and *Thomomys townsendii* in the Honey Lake Valley region of northeastern California. His study encompassed a multivariate morphometric assessment of cranial and pelage color characters, and he clearly demonstrated presumptive hybrid individuals based on morphological intermediacy. The possibility of limited gene exchange between the two species was thus raised. In his study, Thaeler compared the extent of hybridization between *bottae* and *townsendii* with that between intergrading subspecies of *T. bottae* in central California, using the differential extent of hybrid formation as a basis for making judgements as to specific status. Hall (1981), citing Thaeler's results, considered *townsendii* to be conspecific with *bottae* (but used the name *umbrinus*), based on his view (Hall 1943a,b, 1981:viii–ix) that any hybridization between taxa indicates a lack of reproductive isolation and thus conspecific populations.

In a series of reports examining the nature of genetic and reproductive interactions in a range of hybrid zones of the *Thomomys bottae* group of pocket gophers, we have attempted to draw the distinction between reproductive and genetic isolation between taxa, and have provided a set of operational criteria for defining species limits in situations of hybrid formation (see Patton et al. 1979, Patton 1981). We have argued that when hybrid formation is restricted to the F_1 generation, genetic isolation is complete even though reproductive isolation is not. From an evolutionary standpoint, the degree of genetic isolation is the significant component in any assessment of the systematic status of particular hybrid situations. Thus, the species *T. bottae* and *T. umbrinus* are genetically (and evolutionarily) separate units although they form occasional hybrids at one point of parapatric contact (Patton et al. 1972, Patton 1973). In contrast, the various morphologically, karyotypically, and/or genically differentiated units of *T. bottae* that have been examined at points of contact show wide ranges of backcross hybrid formation, with genic introgression extending beyond the limits of a morphologically and ecologically defined hybrid zone (e.g., Colorado River [Smith and Patton 1981]; White-Sacramento Mountains [Patton et al. 1979]; Rio Grande Valley [Smith et al. 1983]; Sangre de Cristo Mountains [Hafner et al. 1983]). Such evidence for genic introgression fully supports the view that these populations belong to but a single biological species. In these cases, neither reproductive nor genetic isolation is present.

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Thaeler's (1968:548, Fig. 1) morphological analysis suggested a population composition of about 20–30% hybrid individuals at two areas of contact between *T. bottae* and *T. townsendii* in the Honey Lake Valley region in Lassen County, California: Gold Run Creek south of Susanville (between *T. b. saxatilis* and *T. t. relictus*) and Garnier Ranch to the southeast of Honey Lake (between *T. b. canus* and *T. townsendii relictus*). This estimate is considerably higher than the 11–15% hybrid proportion in the contact between *T. bottae* and *T. umbrinus* in Arizona (Patton 1973) but is substantially lower than that between fully intergrading subspecies of *T. bottae* (e.g., *T. b. pascalis* and *T. b. mewa* in central California, >76% [Thaeler 1968]; *T. b. actuosus* and *T. b. ruidosae* in south central New Mexico, >81% [Patton et al. 1979]). The extent of *bottae* x *townsendii* hybridization and Thaeler's (1968) recognition of possible backcross hybrid individuals suggests that genetic isolation may not be complete between these taxa. This raises the possibility that Hall's (1981) view regarding conspecificity of these forms may be correct.

We have approached this problem by combined genetic and morphological analyses of specimens from the contact zone of *bottae saxatilis* and *townsendii relictus* in Gold Run Creek. Genetic studies were limited to electromorphic analysis of protein variation; the morphological analysis incorporated a multivariate assessment of the placement of genetically known individuals to which could be compared the series originally examined by Thaeler, for which no genetic data are available. Additionally, an independent perspective of the geographic extent of potential introgression was obtained by examining the distribution of mallophagan lice on gopher specimens collected in the Gold Run Creek area. Parental populations of *townsendii* and *bottae* serve as hosts for *Geomydoecus idahoensis* and *G. shastensis*, respectively, both of which are included in the *oregonus* complex by Price and Hellenthal (1980). Previous investigations of *Geomydoecus* lice have shown them to exhibit a high degree of host specificity and to support genetically based separations of gopher populations (Hellenthal and Price 1976).

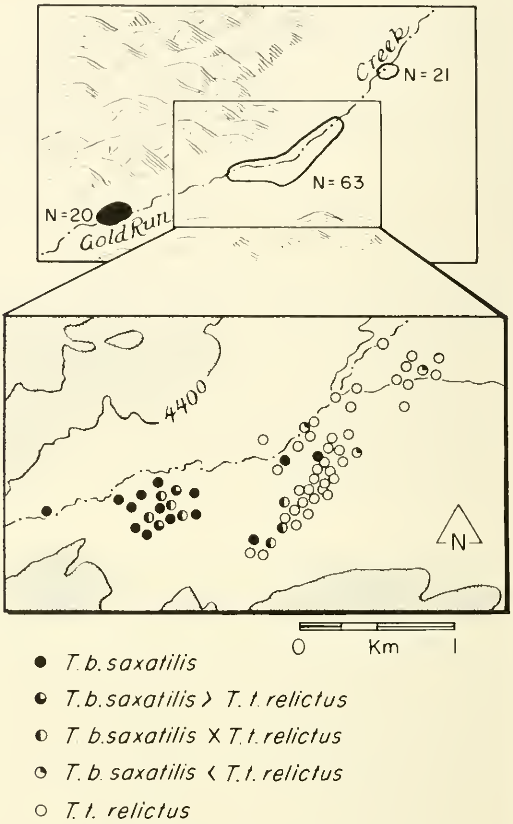
Creek
N = 21
N = 63
N = 20
Gold Run
4400
N
0 Km 1
● T. b. saxatilis
T. b. saxatilis > T. t. relictus
T. b. saxatilis X T. t. relictus
T. b. saxatilis < T. t. relictus
○ T. t. relictus

Fig. 1. Map of Gold Run Creek south of Susanville, Lassen County, California, showing location of parental *Thomomys bottae saxatilis* and *T. townsendii relictus* samples and hybrid zone. Inset: detailed map of hybrid zone showing trap localities of individual pocket gophers collected; genetic parents, F_1, and backcross hybrids are indicated.

MATERIALS AND METHODS

ELECTROPHORESIS.— 104 individuals from Gold Run Creek formed the basis for the majority of the analysis reported here. These include: (a) 20 specimens of presumptive *T. b. saxatilis* trapped at the head of Gold Run Creek, about 1.5 miles above the hybrid zone defined by Thaeler (1968); (b) 21 specimens of presumptive *T. t. relictus* trapped about 1 mile northeast of the mouth of Gold Run Creek; and (c) 63 individuals from within the hybrid zone along the lower reaches of Gold Run Creek (Fig. 1). Sample (a) was collected during a single day in June 1981; samples (b) and (c) were collected over a five-day period in March 1982. Additional specimens of *townsendii* were available from the eastern end of Honey Lake Valley (Garnier Ranch [N = 14] and vicinity of Herlong [N = 44]) and from Standish (N = 18), about 14 miles to the east of Susanville. The additional specimens are from Patton and Yang (1977) and Rogers (1983).

Electrophoretic procedures followed those used in previous studies with *Thomomys* pocket gophers (e.g., Patton et al. 1972, Patton and Yang 1977, Smith and Patton 1981). Twenty-five presumptive loci were examined for population samples of *bottae saxatilis* and *townsendii* trapped away from the hybrid zone to identify those loci with alleles diagnostic to the two taxa (LDH-1 and -2, MDH-1 and -2, IDH-1 and -2, GOT-1 and -2, αGPD, IPO, Pept-1, SDH, 6PGD, PGM, PGI, ADH, Est-4, ADA, Ga3PDH, Alb, pre-Alb, Trf, MPI, Acon-1, and NP). Only those loci so diagnostic were examined for individuals trapped within the hybrid zone.

Morphometrics.— Morphological variation was examined for 14 cranial variables, as defined in previous studies (Patton et al. 1979, Smith and Patton 1984): occipito-nasal length (ONL), basilar length of Hensel (BaL), zygomatic breadth (ZB), mastoid breadth (MB), least interorbital constriction (IOC), rostral length (RL), nasal length (NL), rostral width (RW), diastema length (DL), maxillary tooth row length (MTRL), palatal width (PW), bullar length (BuL), rostral depth (RD), and incisive procumbancy (PRO). External dimensions were excluded because of the variance in the way individual investigators measure particular characters. Only specimens judged to be adult by criteria of the closure of the basisphenoid-basioccipital and exoccipital-supraoccipital sutures were utilized in the analysis.

Middorsal pelage color characteristics, including relative brightness (= value), excitation purity (= chroma), and dominant wavelength (= hue), were determined by use of a Bausch and Lomb Spectronic 505 recording spectrophotometer with a visible reflectance attachment. Only individuals in adult pelage were examined.

Males and females were treated separately in the analysis of cranial characters due to pronounced sexual dimorphism; both sexes were grouped for the colorimetric analyses.

The level of differentiation between the taxa in question and the possibility of individuals of morphological intermediacy were examined by the multivariate techniques of principal components and discriminant function analyses, using the program packages from MBS Consulting and SPSS (Nie et al. 1975), respectively, with the CDC 6400 computer at the University of California at Berkeley.

Host parasite association.— Lice were collected by brushing the gopher skin and were subsequently mounted on microslides and identified to species without prior knowledge of host identification or genetic information. Host parasite association and locality data obtained in this study were evaluated using a computerized taxonomic and geographic analysis system maintained on an IBM 370/168 computer at the University of Notre Dame (see Hellenthal and Price 1980). Mounted lice are deposited in the University of Minnesota insect collection.

Results and Discussion

Genic variation, hybrid formation, and introgression.— Samples of *T. b. saxatilis* from the head of Gold Run Creek (N = 20) differ by apparently fixed alleles at five loci when compared to those of *T. t. relictus* collected from Standish and the southeastern parts of Honey Lake Valley (combined N = 76): 6PGD, αGPD, NP, Acon-1, and pre-Alb. At an additional three loci (Trf, Est-4, and ADH), although the same dominant allele characterizes both taxa, secondary alleles were restricted to one or the other (Table 1). This set of loci can be used, therefore, as genetic markers to identify unequivocally F_1 as well as likely subsequent filial and backcross generation hybrids from the sample available from Gold Run Creek.

Genic hybrid index scores based on the genotypes of each individual for the five diagnostic loci are shown in Figure 2 (see Patton et al. 1979 and Smith and Patton 1981 for calculation of this index). When all individuals sampled from the Gold Run Creek area are combined (N = 104), the majority (88.5%) have hybrid index scores indicative of either parental *bottae* or *townsendii*, and only 11.5% are grouped as genetic intermediates (hybrid indices of 0, +2, +4, etc.). Seven of these presumptive hybrids are exactly intermediate, suggesting that they are F_1 individuals; the remainder are heterozygous at one or more of the diagnostic loci and homozygous for one parental allele or the other at additional loci. Clearly, hybridization between *bottae* and *townsendii* along Gold Run Creek is minimal in amount and is largely limited to F_1 production. The proportion of hybrids in our genetic samples is lower than that suggested by Thaeler (1968) from his morphological analysis of this zone (20–30%). However, the pattern we observed is identical to that seen in the hybridization between *T. bottae* and *T. umbrinus* in southern Arizona, where F_1 males are sterile and F_1 females show greatly reduced fertility (Patton 1973). It contrasts markedly with cases of hybridization leading to extensive genic introgression in contact zones within *T. bottae* (see Patton et al. 1979, Smith et al. 1983, Hafner et al. 1983).

Hybridization at Gold Run Creek is not limited, however, to F_1 production, suggesting that F_1 individuals of either or both sexes are at least partially fertile and that genetic isolation between the parental forms may not be complete. Nevertheless, no evidence of genic introgression extending beyond the immediate vicinity of the hybrid zone is available. No genetic characteristics of either parental form are seen in samples of the opposite taxon trapped at distances of about one mile from the location of hybrids in Gold Run Creek. This is true even though reproductive data indicate that hybrid individuals of both sexes have normal reproductive characteristics. Testis length, seminal vesicle length, and epididymal tubule diameter did not differ between hybrid males and those of either parent. Similarly, the only reproductively active adult female hybrid trapped contained five embryos of late term, a litter size characteristic of both species.

The reason for failure of genic introgression between the two taxa, therefore, is not at all understood. Clearly, available data do not suggest severe F_1 or backcross hybrid fertility or viability barriers, as is the case in *T. bottae* and *T. umbrinus* (Patton 1973). Limitation of introgression is, therefore, likely to be mediated by behavioral interactions determining both spatial territorial relationships and mating preferences. Spatially, the two taxa overlap only minimally

TABLE 1. Allele frequencies at eight diagnostic loci for samples of *T. bottae saxatilis* and *T. townsendii relictus* from Honey Lake Valley, Lassen County, California.

		Saxatilis	*Relictus*		
Locus	Allele	Upper Gold Run Creek (N = 20)	Mouth Gold Run Creek (N = 21)	Standish (N = 18)	Herlong/ Garnier Ranch (N = 44)
αGPD	119	1.00			
	100		1.00	1.00	1.00
NP	107	1.00			
	100		1.00	1.00	1.00
6PGD	100	1.00			
	88		1.00	1.00	1.00
Acon-1	117	1.00			
	100		1.00	1.00	1.00
preAlb	101	1.00			
	100		1.00	1.00	1.00
Trf	130	0.05			
	121	0.95	1.00	1.00	1.00
Est-4	102	0.175			
	95	0.825	1.00	1.00	1.00
ADH	-114	1.00	0.788	0.889	0.412
	-100		0.211	0.111	0.588

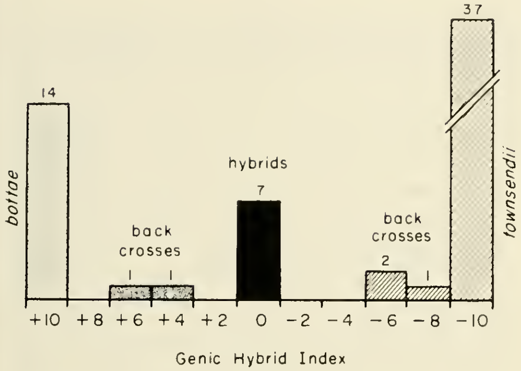

Fig. 2. Distribution of genic hybrid index scores for all specimens examined electromorphically from the hybrid zone along Gold Run Creek. Parental *bottae* and *townsendii* have +10 or −10 scores, respectively; F_1 hybrids are exactly intermediate with a score of 0; and those few specimens with scores between 0 and either +10 or −10 are considered genic backcrosses.

over but a few hundred meters (see Figure 1). Indeed, except for three *bottae* individuals, the two taxa were almost exclusive in their distributions along Gold Run Creek in 1982.

Morphological differentiation and hybrid intermediacy.— The morphological relationships of *bottae* and *townsendii* and their hybrids through the Gold Run Creek contact zone were examined from both colorimetric and cranial morphometric perspectives. In the former case, analysis was restricted to genically known individuals, and cranial character variation was assessed for the genetic samples as well as those collected in previous years, including the material examined by Thaeler in his 1968 study.

Variation for the three dorsal color variables measured is given in Table 2. The total sample was arranged into parental *townsendii* and *bottae*, genic F_1 hybrids, and presumptive backcross hybrids. The two taxa differ significantly ($p < .01$) in both dominant wavelength and brightness, but are inseparable in purity. This color difference is readily appreciated by the eye; *bottae saxatilis* is a rich cinnamon brown above and *townsendii relictus* is a pale yellow-gray. F_1 hybrids are intermediate between the parental forms in both wavelength and brightness, but are slightly skewed toward *bottae* (Fig. 2). The two backcross categories are appropriately intermediate between F_1s and their respective parental types. In general, hybrid class individuals are identifiable as such by eye from their color characteristics.

A principal components (PC) analysis was performed on the 14 cranial variables for all available samples of *townsendii*, *bottae*, and their presumptive hybrids from the Gold Run Creek area. This analysis was designed to determine the nature of differentiation between the taxa as well as to give insight into the morphological relationships of known and presumed hybrids to both parental forms. Only two components are necessary to explain more than 90% of the total variation in the samples (Table 3). Indeed, PCI alone accounts for 84% (males) to 89% (females), with all subsequent components contributing only weakly. All characters, except PRO, load positively and equally on PCI for both males and females. Such uniformity in loadings and the

Table 2. Mean, standard deviation, and range for the three colorimetric variables: dominant wavelength, purity, and brightness for *T. bottae saxatilis*, *T. townsendii relictus*, and their hybrids from Gold Run Creek, near Susanville, California.

Sample	N	Dominant wavelength	Purity	Brightness
Parental *townsendii*	46	582.1 ± 0.82 580–584	18.75 ± 2.42 15.00–23.44	12.81 ± 1.30 8.45–15.24
Backcross to *townsendii*	3	582.7 ± 0.58 582–583	17.52 ± 2.25 14.92–18.93	11.67 ± 0.90 10.86–12.63
F_1 hybrids	7	584.9 ± 1.21 583–586	21.68 ± 4.84 17.47–31.62	9.13 ± 0.73 8.35–10.52
Backcross to *bottae*	2	584.5 ± 0.71 584–585	14.32 ± 2.71 12.40–16.23	8.08 ± 0.08 8.02–8.14
Parental *bottae*	28	585.2 ± 2.03 583–594	17.55 ± 3.55 10.17–26.74	7.90 ± 1.32 5.36–11.57

high proportion of explained variance by PCI suggest that it is primarily a size axis, and that *townsendii* and *bottae* differ cranially predominantly by overall size in combination with differential incisor procumbancy; *bottae* with its small size has a more pronounced procumbancy (see character means, Table 3). There is apparently little marked shape change involved in the size differences in the skulls of *bottae saxatilis* and *townsendii relictus*, at least as identified by linear measurements.

The technique of step-wise discriminant function (DF) analysis was used to examine more closely the morphological relationship between the presumptive hybrids and both parental taxa. In this analysis, genetically known "pure" parental individuals of both taxa were used as a priori groups to which were compared individuals classed as hybrids by their respective genic index scores. In addition, specimens in the MVZ collections, including those examined by Thaeler in his 1968 study, were similarly compared to the parental reference series. This group included individuals identified morphologically as parental, "intermediate" hybrid, or hybrids closer to one or the other parental form (see Thaeler 1968:547).

The standardized discriminant functions for each variable are given in Table 3. Again, major discrimination is achieved by size alone, with ONL loading most highly for both males and females. Since most of the remaining variables are highly correlated with ONL (r = .83 or higher in all cases, with the exception of PRO in both males and females), the high discriminating power of this variable reflects the overall size difference between *bottae saxatilis* and *townsendii relictus*.

Complete separation of the two genetically parental groups is apparent for both sexes in the DF analysis (Fig. 4). Those specimens identified by Thaeler previously as parental *bottae* or *townsendii* are grouped, with no exceptions, with their genetically known counterparts. Thus, the morphological distinctness of the two taxa is unambiguous. Genetic hybrids are generally intermediate between the parental forms in DF score. This is true for all F_I hybrids of both sexes. Although the presumptive backcross individuals all show DF scores in the direction of the parental form involved in the backcrossing, some of these fall in the middle of the parental cluster and would not, therefore, be recognized as possible backcross individuals were it not for the electromorphic data. All specimens identified as possible hybrids by Thaeler are also intermediate in this analysis (Fig. 3).

Distribution of *Geomydoecus* lice.— *Thomomys b. saxatilis* and *T. t. relictus* serve as hosts for the chewing lice *Geomydoecus*

Table 3. Character means for parental samples of *T. bottae saxatilis* and *T. townsendii relictus* from the Gold Run Creek region of Honey Lake Valley south of Susanville, California. Principal component (PC) and discriminant function (DF) loadings are given for each character.

	Character mean *T. bottae*		Character mean *T. townsendii*		PC 1		PC 11		DF	
Variable	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
ONL	40.21	36.62	48.44	44.79	.289	.280	.072	.084	-6.96	4.61
BaL	36.45	32.79	43.00	39.71	.285	.279	.141	.133	2.93	2.20
ZB	28.12	24.60	31.18	28.85	.270	.277	.286	.208	1.88	-2.59
MB	21.29	19.07	26.10	24.16	.285	.280	.017	.047	-3.53	1.99
IOC	6.43	6.46	7.03	7.11	.181	.247	-.626	-.098	-0.73	-0.27
RL	16.66	14.77	20.71	18.49	.270	.280	.127	.056	1.46	-1.71
NL	13.35	11.85	17.51	15.92	.285	.278	.071	.039	1.24	0.48
RW	7.80	6.65	9.92	9.04	.288	.278	.004	-.038	-0.65	2.10
DL	16.29	14.15	18.42	16.47	.264	.258	.316	.375	0.45	-1.80
MTRL	8.31	7.87	10.09	9.49	.270	.259	-.081	-.086	-0.34	1.44
PW	7.52	7.21	8.68	8.34	.275	.272	-.150	-.025	0.16	-0.71
BuL	7.18	6.95	8.37	8.03	.278	.266	.010	-.063	-0.58	-0.37
RD	7.20	6.38	8.59	7.80	.283	.276	.030	.006	-0.04	-0.36
PRO	4.24	3.98	2.61	2.56	-.198	-.201	.592	.873	-0.44	-0.45
				Eigenvalue	11.80	12.49	0.98	0.60		
				% contribution	84.28	89.19	7.01	4.29		

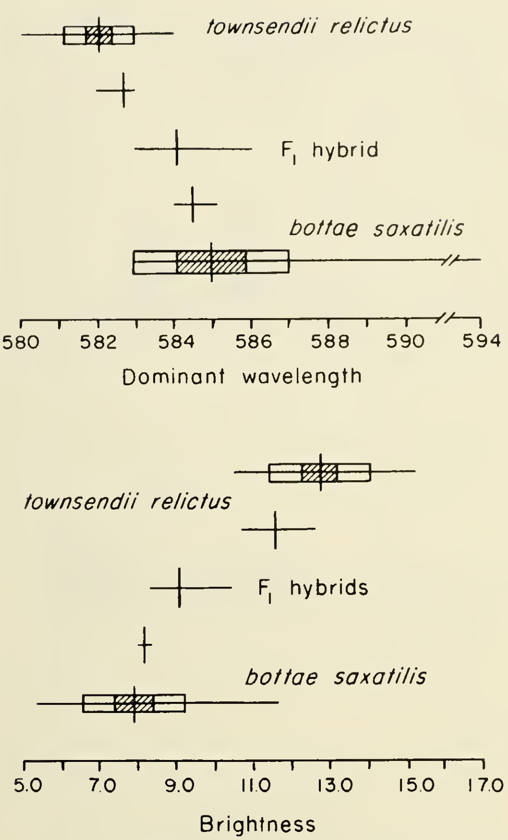

Fig. 3. Colorimetric relationships between *bottae* and *townsendii* and their hybrids from Gold Run Creek. Horizontal bar equals range; vertical bar sample mean; open box one standard deviation and hatched box twice the standard error of the mean.

shastensis and *G. idahoensis*, respectively. *Geomydoecus shastensis* has been collected from 12 subspecies of *T. bottae* representing 200 localities in northern California and southwestern Oregon. In only 5 of these localities were gophers found to also have another species of *Geomydoecus* louse. One of these was the *saxatilis-relictus* hybrid zone, and the remaining 4 involved 5 gophers with *G. angularis*. *Geomydoecus idahoensis* has been collected from 7 subspecies of *T. townsendii* representing 52 localities from northwestern California, southeastern Oregon, northern Nevada, and southern Idaho. In 4 of these localities, gophers were found to also have another *Geomydoecus* species, one of these being the *saxatilis-relictus* hybrid zone under consideration here. Two of the remaining localities were in the Garnier Ranch area east of Honey Lake, where Thaeler (1968) conducted his study of the *T. b. canus* and *T. t. relictus* hybrid zone. Of the 10 gophers examined for lice from these localities and regarded by Thaeler as *canus-relictus* hybrids, 3 had only *G. shastensis*, 2 had only *G. centralis*, and 5 had both louse species. One additional locality in central Nevada also had one gopher with both of these louse species.

The distribution of louse taxa on pocket gophers through the *saxatilis-relictus* hybrid zone in Gold Run Creek thus serves as an independent view of the genetic and ecologic interactions of their hosts. Seventy-one of the genetically determined individuals were found to have lice, and the relationship between louse distribution and gopher taxon is given in Table 4. Three of 46 *relictus* specimens contained only *saxatilis* lice, and the remainder contained only *relictus* lice. All *saxatilis* trapped outside the hybrid zone had only *saxatilis* lice, and of the 13 individuals in the hybrid zone, 6 had only *saxatilis* lice and 7 had both species of lice. All *relictus* trapped outside the hybrid zone, except those from the *canus-relictus* contact to the east, had only *relictus* lice. The presumptive backcross individuals to *townsendii* had only the lice of that species; all other hybrid class individuals had either only *saxatilis* lice or both louse species. It is important that the geographic overlap of the distribution of the two louse species corresponded exactly with the middle of the hybrid zone, as defined by the genetic and morphologic characters of the gopher hosts. As with the electromorphic characters, there is no evidence of a louse species extending into the parental population of the opposite gopher host. The fact that some genetic "pure" gopher parental forms from the hybrid zone have the louse of the other gopher taxon is not unexpected. Lice are probably transferred among individuals by direct contact, which must occur if hybridization is to take place.

SYSTEMATIC AND EVOLUTIONARY CONCLUSIONS

Thomomys bottae and *T. townsendii* do hybridize where they meet along Gold Run Creek south of Susanville, California. The parental taxa differ by fixed alleles at five gen-

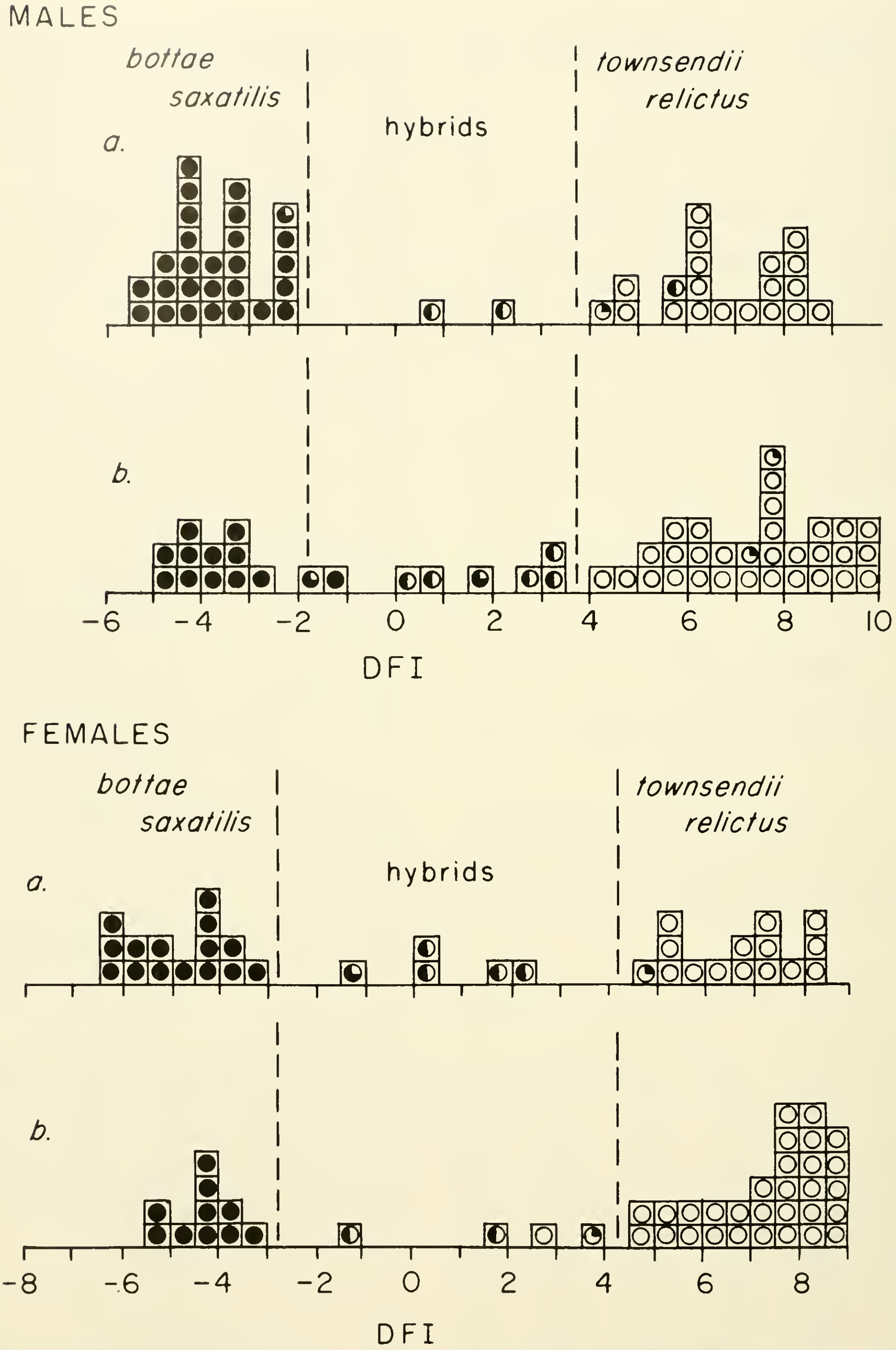

Fig. 4. Distribution of adult specimens from Gold Run Creek along the first discriminant axis for cranial characters. For both males and females, histogram *a* represents specimens for which no genic data are available, including those examined by Thaeler in 1968; *b* represents those specimens for which the hybrid or parental status is based on electromorphic characters (see text). Symbols in *a* indicate hybrids identified on morphological grounds by Thaeler (1968); those in *b* are based on genic data as in Fig. 1.

etic loci, facilitating the recognition of hybrid individuals and the extent of genic introgression. This hybridization is of limited scope; only 12 of 104 specimens (11.5%) examined electromorphically could be considered of hybrid origin. However, both F_1 and presumptive backcross hybrids were identified. If backcrossing occurs, then the F_1 hybrids must be at least partially fertile, and genic introgression between the parental forms is a possibility. In the present case, however, there is no evidence for introgression into parental populations of both taxa less than a mile distant from the hybrid zone. Although the hybrids appear reproductively competent, they must be at a decided disadvantage in competition for mates of either parent. Otherwise some genetic exchange between the two taxa would be expected.

F_1 hybrid individuals are intermediate in morphology, both cranially and in color characters; presumptive backcross individuals are skewed away from intermediacy in the direction of the parental form with which they share greater genetic similarity. This suggests that the genetic differences between the two taxa underlying the morphology are relatively simple and additive. Since so few intermediate individuals were found in samples collected at three intervals over a 25-year period (1960, 1969, and 1982), hybridization must be a sporadic event.

Importantly, genic, cranial, and color scores for any given hybrid are all concordant and intermediate, suggesting that hybridization is limited to the F_1 and but one or two subsequent filial or backcross generations. Repeated backcrossing would cause random assortment of these characters among a hybrid class of individuals, unless the controlling genetic elements were tightly linked. The latter is unlikely since the genome of both taxa consists of at least 38 linkage groups (i.e., the diploid number is 76 in both cases). Thus, the *bottae-townsendii* data contrast sharply with those from the *bottae actuosus* and *bottae ruidosae* hybrid zone in the White-Sacramento Mountains of New Mexico, for example, where two units likewise meet and hybridize along a narrow mountain canyon. In this case, hybridization is extensive because most individuals are various combinations of genetic backcrosses, with morphological and genic scores strongly discordant in many, indicating rather random reassortment of the parental characters.

The systematic and evolutionary significance of hybridization stems not from the lack of complete reproductive isolation between taxa, but rather in the presence of genetic isolation (Patton 1973, 1981; Patton et al. 1979). Since hybridization per se does not automatically produce actual gene exchange between the hybridizing forms, it is the degree of genetic rather than reproductive isolation that should be the measure of species status in hybrid situations. In the present case, *bottae* and *townsendii* are genetically isolated despite minimal hybridization over at least the past 25 years; there is simply no genic or morphologic evidence suggestive of introgression into either parental population, even at distances of a mile or less from the hybrid zone. Consequently, *bottae* and *townsendii* are evolutionarily separate units, and as such should be accorded full species status (contra Hall 1981).

Table 4. Distribution of *Geomydoecus* lice on pocket gopher host taxa through the contact zone between *Thomomys bottae saxatilis* and *Thomomys townsendii relictus* along Gold Run Creek. *T. bottae* is the host of *G. shastensis*, and *T. townsendii* is the host for *G. idahoensis*.

	Lice		
Gopher:	*G. idahoensis*	*G. shastensis*	Both
T. townsendii	43	3	0
Backcross to *T. townsendii*	3	0	0
F_1 hybrid	0	3	4
Backcross to *T. bottae*	0	1	1
T. bottae	0	6	7

Acknowledgments

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LITERATURE CITED.

HAFNER, J. C., D. J. HAFNER, J. L. PATTON, AND M. F. SMITH. 1983. Contact zones and the genetics of differentiation in the pocket gopher, *Thomomys bottae* (Rodentia: Geomyidae). Syst. Zool. 32:1–20.

HALL, E. R. 1943a. Intergradation versus hybridization in ground squirrels of the western United States. Amer. Midl. Nat. 29:375–378.

______. 1943b. Criteria for vertebrate subspecies, species and genera: the mammals. Ann. N.Y. Acad. Sci. 44:141–144.

______. 1981. The mammals of North America. Vol. 1, 2d ed. John Wiley & Sons, Inc., New York. 600 + 90 pp.

HELLENTHAL, R. A., AND R. D. PRICE. 1976. Louse-host associations of *Geomydoecus* (Mallophaga: Trichodectidae) with the yellow-faced pocket gopher, *Pappogeomys castanops* (Rodentia: Geomyidae). J. Med. Entomol. 13:331–336.

______. 1980. A review of the *Geomydoecus subcalifornicus* complex (Mallophaga: Trichodectidae) from *Thomomys* pocket gophers (Rodentia: Geomyidae), with a discussion of quantitative techniques and automated taxonomic procedures. Ann. Entomol. Soc. Amer. 73:495–503.

NIE, H. N., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences. McGraw-Hill Book Co., New York. 675 pp.

PATTON, J. L. 1973. An analysis of natural hybridization between the pocket gophers, *Thomomys bottae* and *Thomomys umbrinus* in Arizona. J. Mammal. 54:561–584.

______. 1981. Chromosome and genic divergence, population structure and speciation potential in *Thomomys bottae* pocket gophers. Pages 255–295 *in* O. A. Reig, ed., Ecologia y genetica de la especiación animal. Equinoccio, Caracas, Venezuela.

PATTON, J. L., J. C. HAFNER, M. S. HAFNER, AND M. F. SMITH. 1979. Hybrid zones in *Thomomys bottae* pocket gophers: genetic, phenetic, and ecologic concordance patterns. Evolution 33:860–876.

PATTON, J. L., R. K. SELANDER, AND M. H. SMITH. 1972. Genic variation in hybridizing populations of gophers (genus *Thomomys*). Syst. Zool. 21:263–270.

PATTON, J. L., AND S. Y. YANG. 1977. Genetic variation in *Thomomys bottae* pocket gophers: macrogeographic patterns. Evolution 31:697–720.

PRICE, R. D., AND R. A. HELLENTHAL. 1980. The *Geomydoecus oregonus* complex (Mallophaga: Trichodectidae) of the western United States pocket gophers (Rodentia: Geomyidae). Proc. Entomol. Soc. Washington 82:25–38.

ROGERS, M. A. 1983. Evolutionary differentiation within the northern Great Basin pocket gophers, *Thomomys townsendii*. Unpublished thesis. Univ. of California, Berkeley. 199 pp.

SMITH, M. F., AND J. L. PATTON. 1980. Relationships of pocket gopher (*Thomomys bottae*) populations of the lower Colorado River. J. Mammal. 61:681–696.

______. In press. Dynamics of morphological differentiation: temporal impact of gene flow in pocket gopher populations. Evolution.

SMITH, M. F., J. L. PATTON, J. C. HAFNER, AND D. J. HAFNER. 1983. *Thomomys bottae* pocket gophers of the central Rio Grande Valley, New Mexico: local differentiation, gene flow, and historical biogeography. Occas. Papers 2. Museum Southwestern Biol., Univ. of New Mexico, Albuquerque. 16 pp.

THAELER, C. S., JR. 1968. An analysis of three hybrid populations of pocket gophers (genus *Thomomys*). Evolution 22:543–555.

VEGETATION PARAMETERS FOR JUDGING THE QUALITY OF RECLAMATION ON COAL MINE SPOILS IN THE SOUTHWEST

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Abstract.— Mining reclamation specialists and government regulators need sound criteria for judging when reclamation is complete and expensive bonds can be released. Values are given for five easily measured plant parameters that can be used for judging success on native species that are growing on semiarid grasslands and sagebrush lands.

The federal Surface Mining Control and Reclamation Act of 1977, along with the many state reclamation laws and Indian tribal regulations, have done much to protect the areas whose jurisdiction they encompass. Some additional needs remain: How are these reclaimed areas to be managed after mining and reclamation are complete? And just when is reclamation complete? This latter question is of no small consequence. Often thousands of dollars are tied up in bonding requirements mandated by law. Mining companies are acutely aware of these costs for they must bear them until "reclamation is complete" and their bonds are released. Land managers are concerned, for it is they who must decide when the area has been restored to a condition that can safely perpetuate itself for years to come with minimum adverse effects. Some information based on research and field experience is available at present for making these decisions. More such information is needed. This paper outlines a range of several vegetation parameters, found on unmined areas of the Four Corners coal province of the United States, that should assist managers working in this area in deciding when vegetation on reclaimed lands has reached unmined levels.

Some Constraints

The vegetation component of an ecosystem is dynamic, and subject to a wide variety of forces. To freeze this movement with a single value and call that number final would be misleading. The range of numbers reported here are to be used as guides, not absolutes. These data can be used to tell whether a reclaimed stand is far below what might be expected from natural, but not protected, stands.

The vegetation parameters chosen and reported on here (cover, density, frequency, importance value, and diversity) are the ones used presently in the course of a study (Rio Puerco, see below) on understanding the effect of grazing systems on semiarid vegetation changes. Other valid parameters used in ecological research could have been chosen and reported on from the literature. The ones used here are common to rangeland research and easily obtained in the field.

Native species only are reported here. There are many other species being used in reclamation in the Southwest at present. To make comparisons between importance values of differing species would be hazardous. Care must be taken when any comparisons are made. Cover and density comparisons between stands are less likely to lead to problems.

Age of stands are not considered here. The number of growing seasons required to be assured of stability is not certain, but it has been reported two growing seasons are needed for stand establishment and seven years to demonstrate long-term survival (Aldon 1981).

The only vegetation associations considered here are the sagebrush series in the Great Basin desertscrub biome and the sacaton series in the Great Basin shrub–grasslands biome (Brown et al. 1979). Two other vegetation types, pinyon-juniper series in the Great

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Basin conifer-woodland biome, and the shadscale series of the Great Basin desertscrub biome, are widespread in the Southwest and will need additional data.

Methods

Vegetation sampling.— The Community Structure Analysis (CSA) method has been used throughout (Pase 1980). The CSA method was used to estimate the relative position of a plant species within the community by an Importance Value (IV). The IV is based on the sum of the relative values for cover, density, and frequency for each species in the stand. The sum of the IVs for all species in a stand, then, is 3. The computed IV is little affected by year-to-year fluctuations in precipitation, shows minor differences between observers, and changes indicate change in range

Table 1. Cover, density, diversity values for two vegetation types.

	1979	1980	1981	All years
		Vegetation type 1 Semiarid grassland		
	128	122	124	374 transects
Cover (%)				
Median	17.6	14.9	18.6	17.3
Mean	19.6	16.8	18.8	18.4
Standard deviation	8.2	7.3	7.1	7.6
Minimum value°	6.5	5.3	5.6	5.3
Maximum value°	47.5	50.4	40.2	50.4
Density (plants/m²)				
Median	27.3	40.5	29.2	31.2
Mean	32.8	47.6	32.1	37.4
Standard deviation	19.0	29.1	20.4	24.2
Minimum value	2.3	3.6	5.3	2.3
Maximum value	104.8	171.2	105.7	171.2
Diversity (Index Values)				
Median	1.3	1.2	1.2	°°
Mean	1.3	1.2	1.2	
Standard deviation	0.4	0.4	0.3	
Minimum value	0.4	0.4	0.4	
Maximum value	2.1	2.4	2.1	
		Vegetation type 2 Sagebrush grass		
	48	53	53	154 transects
Cover (%)				
Median	23.2	20.9	23.2	21.8
Mean	22.0	20.7	22.6	21.8
Standard deviation	7.3	5.4	6.9	6.6
Minimum value	0.1	10.8	6.1	0.1
Maximum value	37.0	35.3	43.5	43.5
Density (plants/m²)				
Median	43.8	57.4	29.8	41.2
Mean	46.3	56.8	31.7	44.9
Standard deviation	22.8	27.5	14.3	24.4
Minimum value	1.9	3.3	8.3	1.9
Maximum value	105.8	124.9	60.4	124.9
Diversity (Index Values)				
Median	1.6	1.6	1.4	°°
Mean	1.5	1.5	1.3	
Standard deviation	0.5	0.4	0.5	
Minimum value	0.5	0.6	0.3	
Maximum value	2.3	2.3	2.1	

°Actual values used throughout
°°Data not subject to averaging

condition (Pase 1980). Cover is based on 100 measurements taken along a 200-m transect randomly located in the field using a 5 x 10 cm rated microplot (Morris 1973). Cover is determined by rating or scoring the area occupied by plants inside this small plot. Density is based on individual plants per m² taken on 10 circular plots along the same transect. Frequency is the relative number of "stocked" m² circular plots. Rock, litter, and bare soil values are also estimated in the microplot. These latter values are not reported here, but are available from the author.

The diversity index is calculated for each plant array based on absolute density. The index, as used here, is computed from the density of individual species as a proportion of the total density and the total number of species in the community (MacArthur and MacArthur 1961).

The CSA method and diversity index are computerized, and this program is available from the author. Detailed field methods are also available.

Sampling areas.— Data presented here are taken from a long-term grazing study located on the Rio Puerco drainage in north central New Mexico (for a complete discussion, see USDI Bureau of Land Management 1978). The 159,199 hectares of public lands in this area are divided into 75 grazing allotments, varying in size from 39 hectares to more than 2,025 hectares. Nine representative allotments, distributed evenly over the entire area, were selected for detailed study. Each allotment is divided into three to five pastures. Most pastures have four or five CSA transects located randomly on key grazing areas or primary range lands within them, giving a total of 177 transects placed on the nine study allotments. Of these, 176 are used in this paper. The transects were installed and read in the summer of 1979. They were reread in the summers of 1980 and 1981. Most of the sampling areas are considered in fair to poor range condition at present; thus the values will be on the lower end of a continuum. But precipitation over the area was considered above average for 1979 and 1981, and average in 1980, thus providing maximum vegetation outputs in those better years.

Study allotment description.— The allotments range from pinyon-juniper woodlands with a scattering of ponderosa pine at higher elevations down to semiarid grasslands. The area is composed of mesas or uplands, steep rocky breaks, and alluvial grasslands. A layer of Mesa Verde sandstone overlies Mancos shale. The sandstone breaks

Table 2. Importance Value for three plant species.

	Vegetation type 1			Vegetation type 2		
	1979	1980	1981	1979	1980	1981
Alkali sacaton						
Median	0.451	0.517	0.420	0.114	0.065	0.027
Mean	0.614	0.613	0.626	0.105	0.062	0.083
Standard deviation	0.536	0.516	0.588	0.095	0.044	0.122
Minimum value	0.001	0.002	0	0.010	0.001	0.004
Maximum value	2.322	1.981	2.319	0.249	0.121	0.357
Number of transects	91	81	83	5	9	9
Galleta						
Median	0.692	0.686	0.561	0.152	0.260	0.261
Mean	0.754	0.712	0.670	0.222	0.292	0.288
Standard deviation	0.496	0.469	0.491	0.183	0.207	0.210
Minimum value	0.002	0.001	0.001	0.004	0.006	0.008
Maximum value	2.112	1.862	1.805	0.663	0.660	0.815
Number of transects	106	104	105	32	34	33
Blue grama						
Median	0.432	0.493	0.513	0.914	0.795	0.778
Mean	0.608	0.666	0.659	0.905	0.762	0.881
Standard deviation	0.540	0.572	0.542	0.506	0.441	0.532
Minimum value	0.004	0.001	0.003	0.089	0.045	0.013
Maximum value	1.904	1.946	2.028	1.890	1.683	2.144
Number of transects	108	105	108	46	50	49

and underlying shales form the parent soil material, the texture of which varies from sandy loam to silty clay. Coal seam outcrops are prevalent, and there is one active surface mine in operation on the area. Precipitation ranges from 38 cm per year at higher elevations, 2300 m, to 20 cm at the lower elevations, 1500 m.

The areas of pastures sampled in this study fall into two vegetation types: a sagebrush-grass mixture and a semiarid grassland type. The sagebrush-grass type consists of big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata*), blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.), alkali sacaton (*Sporobolus airoides* [Torr.] Torr.), western wheatgrass (*Agropyron smithii* Rydb), with some black greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.) and *Opuntia* spp. scattered throughout. The semiarid type consists mostly of al-

TABLE 3. Frequency for three plant species.

	1979	1980	1981	All years
		Vegetation type 1		
ALKALI SACATON				
Median	0.3	0.3	0.3	0.3
Mean	0.4	0.4	0.3	0.4
Standard deviation	0.3	0.3	0.3	0.3
Minimum value	0	0	0	0
Maximum value	1.0	1.0	1.0	1.0
Number of transects	91	81	83	255
GALLETA				
Median	0.5	0.5	0.4	0.5
Mean	0.5	0.5	0.4	0.5
Standard deviation	0.3	0.3	0.3	0.3
Minimum value	0	0	0	0
Maximum value	1.0	1.0	1.0	1.1
Number of transects	106	104	105	315
BLUE GRAMA				
Median	0.4	0.4	0.4	0.4
Mean	0.4	0.4	0.4	0.4
Standard deviation	0.3	0.3	0.3	0.3
Minimum value	0	0	0	0
Maximum value	1.1	1.0	1.0	1.1
Number of transects	108	105	108	321
		Vegetation type 2		
ALKALI SACATON				
Median	0.1	0.1	0	0.1
Mean	0.1	0.1	0.1	0.1
Standard deviation	0.1	0.1	0.1	0.1
Minimum value	0	0	0	0
Maximum value	0.2	0.2	0.3	0.3
Number of transects	5	9	9	23
GALLETA				
Median	0.3	0.4	0.3	0.3
Mean	0.3	0.4	0.4	0.4
Standard deviation	0.3	0.3	0.3	0.3
Minimum value	0	0	0	0
Maximum value	0.9	0.8	0.9	0.9
Number of transects	32	34	33	99
BLUE GRAMA				
Median	0.8	0.8	0.7	0.8
Mean	0.7	0.7	0.7	0.7
Standard deviation	0.3	0.3	0.3	0.3
Minimum value	0.1	0	0	0
Maximum value	1.0	1.0	1.0	1.0
Number of transects	46	50	49	145

kali sacaton, blue grama, and galleta (*Hilaria jamesii* [Torr.] Benth.) Fourwing saltbush (*Atriplex canescens* [Pursch] Nutt.) and broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt.) are the principal shrubs. All species occur to some extent in both types, but sagebrush is less in evidence in the semiarid grassland type. For the purposes of this study, the importance values of alkali sacaton, blue grama, and galleta will be listed, for these three species are commonly used in reclamation plantings. Other species IV values are available from the author.

RESULTS

The usual statistics for cover, density, and diversity for individual years and all years combined are shown in Table 1. These are listed so a land manager's field data can be compared with those found in this study to see where the data fall along the continuum. The diversity data are not properly subject to averaging. Table 2 lists the importance values for alkali sacaton, galleta, and blue grama for individual years, and Table 3 the frequency values measured for the same three species.

To arrive at a mean or median value and a range of values that might be used as guides, data used to compile Tables 1, 2, and 3 for each of the three years were pooled and 0.95 nonparametric tolerance limits were computed. The lower and upper bounds of these limits contain at least 95% of the population as represented by the sample data. Table 4 gives these tolerance limits.

Based on tolerance limits data, computed median and mean data, and standard deviation values, the values in Table 4 show both the limits and mean data, representing reasonable approximations of field conditions on semiarid grassland and sagebrush grassland unmined sites in the Southwest.

DISCUSSION

A wide variety of data is needed in decision making, but these tables should help a land manager judge the plant components of the reclaimed stands. For example, these values should be of help to land managers as they continually monitor reclaimed stands prior to bond release. If initial seedings fall below these values, replanting should be contemplated. If a dry year occurs and measured values from a reclaimed stand are at the low end of these tables, the stand could still be considered acceptable and able to sustain itself. If several "wet" growing seasons occur in a row and stands are still at the low end of these tables or if importance values shift downward drastically, careful examination of the stands should be made and problems corrected.

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LITERATURE CITED

ALDON, E. F. 1981. Long term plant survival and density data from southwestern coal mine spoils. Great Basin Nat. 41(3):271–3.

TABLE 4. Tolerance limits and means for cover, density, diversity, importance value, and frequency.

	Vegetation type 1 (semiarid grasslands)		Vegetation type 2 (sagebrush grasslands)	
	Limits	Mean	Limits	Mean
Cover (%)	8 to 37	18	11 to 37	22
Density (plants/m^2)	7 to 99	35	8 to 112	42
Diversity	0.57 to 1.92	1.20	0.51 to 2.24	1.45
Importance value (IV)				
Alkali sacaton	0.005 to 1.98	.50	0.001 to 0.36	.27
Galleta	0.016 to 1.75	.70	0.006 to 0.66	.24
Blue grama	0.007 to 1.81	.60	0.067 to 1.89	.85
Frequency				
Alkali sacaton	0 to 1.0	.4	0 to 0.3	.1
Galleta	0 to 1.0	.5	0 to 0.9	.3
Glue grama	0 to 1.0	.4	0 to 1.0	.7

Brown, D. E., C. H. Lowe, and C. P. Pase. 1979. A digitized classification system for the biotic communities of North America, with community (series) and association examples for the Southwest. J. Arizona-Nevada Acad. Sci. 14(Supplement 1):16.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–599.

Morris, M. J. 1973. Estimating understory plant cover with rated microplots. USDA Forest Service Res. Paper RM-104. Rocky Mountain Forest and Range Expt. Station, Fort Collins, Colorado. 12 pp.

Pase, C. P. 1980. Community structural analysis—a rapid, effective range condition estimator for semiarid ranges. Pages 425–430 *in* Arid land resources inventories: developing cost-efficient methods, an international workshop. La Paz, Mexico, Nov. 30–Dec. 6, 1980. General Technical Report WO-28, U.S. Department of Agriculture, Forest Service, Washington, D.C.

USDI Bureau of Land Management. 1978. Final Rio Puerco grazing environmental statement. Albuquerque, New Mexico.

BURROW PLUGGING BY PRAIRIE DOGS IN RESPONSE TO SIBERIAN POLECATS

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Abstract.— Siberian polecats (*Mustela eversmanni*) were placed in white-tailed prairie dog (*Cynomys leucurus*) and black-tailed prairie dog (*C. ludovicianus*) burrows to simulate a black-footed ferret (*M. nigripes*) visit. Both prairie dog species plugged burrows "visited" by polecats. White-tailed and black-tailed prairie dogs plugged 2 of 6 and 3 of 6 test burrows, respectively.

Black-tailed prairie dogs (*Cynomys ludovicianus*) often attempt to cover entrances of burrows occupied or "visited" by black-footed ferrets (*Mustela nigripes*) (Hillman 1968, Henderson et al. 1969). Hillman and Linder (1973) reported that colonies of less than 16.2 hectares occupied by black-footed ferrets might have 15%–25% of the burrows plugged. The response of white-tailed prairie dogs (*C. leucurus*) to the presence of black-footed ferrets is less well known, but Clark (1978) reported that they may not plug burrows occupied by black-footed ferrets. During 1980 we examined the responses of black-tailed and white-tailed prairie dogs to Siberian polecats (*M. eversmanni*). The Siberian polecat is the closest living relative of the black-footed ferret, and the two may be conspecific (Anderson 1977). The objective of this test was to ascertain whether or not white-tailed prairie dogs plug burrows occupied or "visited" by black-footed ferrets and to verify previous observations of this behavior in black-tailed prairie dogs. The results of this study are of significant importance to searchers who conduct surveys for black-footed ferrets in prairie dog colonies.

Methods

Field experiments were divided into two phases: (1) tests on black-tailed prairie dogs in a 6.1-ha colony near Fort Collins, Larimer County, Colorado, and (2) a trial on a 4.1-ha white-tailed prairie dog colony on Hutton Lake National Wildlife Refuge, Albany County, Wyoming.

On each prairie dog colony .4-ha plots were established and divided into two subplots, one treatment and one control. Each subplot pair was independently tested for 3 consecutive days. All burrows in each subplot were examined each morning to determine if plugs were present. Plugs are defined as dirt material that visually blocks or obscures a portion of the burrow system. Typically, plugging material comes from dirt excavated by prairie dogs at the entrance to a burrow. Two burrows were randomly selected on each subplot for testing. A live Siberian polecat, enclosed in an 8.9 x 45.7 cm cylindrical wire hardware cloth cage, was placed in each of two selected burrows in the treatment plot, and an empty cage was placed in two control burrows in early morning before prairie dogs emerged. All cages were inserted completely below ground level. Two persons observed and recorded prairie dog response to caged polecats during each six-hour test period. Observers viewed the prairie dog colony from a parked vehicle or blind with the aid of binoculars and spotting scopes. After six hours the polecats were removed and each plot was reexamined for plugs. The following morning, if no plugs were present in the test burrows, polecats were reinserted into the same burrow. During nine days of testing (three days in each pair of subplots) on each species, we recorded the number of plugged burrows, time of plugging, and

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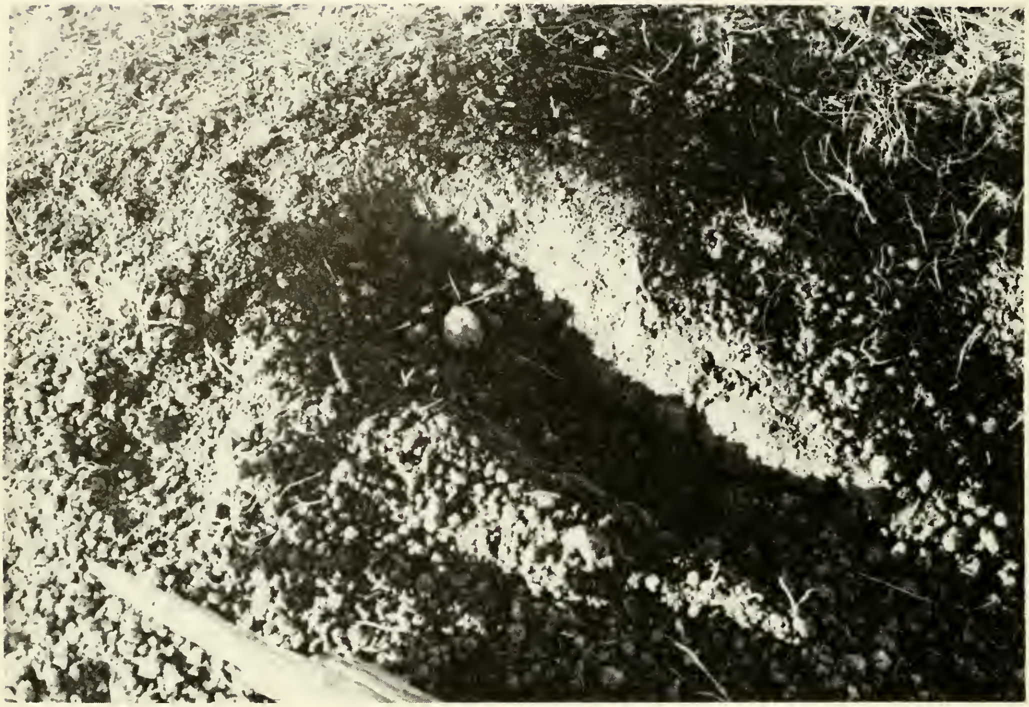

Fig. 1. Burrow plugged by black-tailed prairie dog in response to Siberian polecat.

behavior of prairie dogs in the presence of Siberian polecats.

Results and Discussion

The results revealed that black-tailed and white-tailed prairie dogs plugged 3 of 6 and 2 of 6 burrows, respectively. None of the 12 control burrows were plugged. Plugged burrows (2) were found on one white-tailed and one black-tailed subplot, prior to placement of polecats. No other plugging was observed in nontest burrows.

Black-tailed-prairie-dog-plugged burrows were similar to those photographed on colonies occupied by black-footed ferrets (Henderson et al. 1969). Figure 1 shows a burrow entrance that was completely covered, leaving only an outline of the entrance. Plugs in white-tailed prairie dog burrows differed in being 23–25 cm below the surface, with the burrow entrances more visible. Both species plugged burrows only after the polecats were removed, and during the absence of observers. The interval between when polecats were removed from burrows and when plugging occurred ranged from 6 to 12 hrs. The exact time of plugging is unknown but is believed to have occurred between 1300 and 2100 (MST). Burrows remained plugged for 4–8 days.

Although prairie dogs were not observed plugging burrows, they were seen approaching and responding to caged polecats. Both species of prairie dogs first detected polecat presence by scent, usually at 4.6–6.1 m downwind of the occupied burrow. Upright posture (Smith et al. 1976) characterized this detection and lasted 1–4 minutes. Prairie dogs then slowly walked toward the polecats. When prairie dogs approached within .3–.9 m and visually detected the polecat, they ran away from the hole in the direction of their approach and stood upright again, facing the burrow, and chattered (Smith et al. 1976) for 1–5 minutes. Black-tailed prairie dogs often issued a jump-yip (Smith et al. 1976) response when the polecat was first sighted and again after retreating from the burrow. Henderson et al. (1969) also reported that black-tailed prairie dogs exhibited upright posture, chattering, and jump-yips in response to black-footed ferrets. White-tailed prairie dogs exhibited upright posture and chattering (Clark 1977) but did not jump-yip. Alarm responses from both species had little or no discernible effect on other prairie dogs. No group reactions to the polecats were noted for either species of prairie dog as has been reported for black-tailed prairie dogs and black-footed ferrets in South Dakota (Henderson et al. 1969). The only group reaction was the apparent avoidance of a polecat subplot, which contained two plugged burrows, by black-tailed prairie dogs. Eight prairie dogs moved their activity area approximately 37 m from the vicinity of a previously occupied polecat burrow and did not return during the test period.

These tests indicate that Siberian polecat scent alone doesn't elicit the hole-plugging response in prairie dogs. A visual cue seems necessary since all plugs were in burrows where prairie dogs had visually detected polecats. Woodis (1981) also reported that Siberian polecat scent alone didn't elicit plugging by black-tailed prairie dogs in Colorado.

Test results lead us to believe that both species of prairie dogs may plug burrows occupied or "visited" by black-footed ferrets, but that on occasions no plugging may be found in ferret-occupied colonies. Black-footed ferret searchers should continue to look for plugged burrows but should not rely on this phenomenon as an indicator of the presence or absence of black-footed ferrets.

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LITERATURE CITED

ANDERSON, E. 1977. Pleistocene Mustelidae (Mammalia, Carnivora) from Fairbanks, Alaska. Bull. Mus. Comp. Zool. 148:1–21.

CLARK, T. W. 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Milwaukee Public Mus., Publ. Biol. Geol. No. 3. 97 pp.

______. 1978. Current status of the black-footed ferret in Wyoming. J. Wildl. Manage. 42:128–134.

HENDERSON, R. R., P. F. SPRINGER, AND R. ADRIAN. 1969. The black-footed ferret in South Dakota. South Dakota Game, Fish and Parks Tech. Bull. No. 4. 37 pp.

HILLMAN, C. N. 1968. Field observations of black-footed ferrets in South Dakota. Trans. N. Amer. Wildl. and Nat. Res. Conf. 33:433–443.

HILLMAN, C. N., AND R. L. LINDER. 1973. The black-footed ferret. Black-footed ferret and prairie dog workshop. South Dakota State Univ., Brookings.

SMITH, W. J., S. L. SMITH, J. G. DEVILLA, AND E. C. OPPENHEIMER. 1976. The jump-yip display of the black-tailed prairie dog (*Cynomys ludovicianus*). Animal Behav. 24:609–621.

WOODIS, S. G. 1981. Longevity of simulated ferret trenches on black-tailed prairie dog colonies. J. Colo.-Wyo. Acad. Sci. 13(1):63–64.

DIFFERENTIAL WINTER MORTALITY BETWEEN MALE AND FEMALE MULE DEER FAWNS IN UTAH

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Abstract.— During the winters of 1980–1984 winter mortality of mule deer fawns in central Utah was assessed. It was determined that the winter mortality ratio for female fawns as compared to males was 156:100. This mortality factor should be taken into consideration by game and range managers when determining harvest recommendations.

Among black-tailed deer (*Odocoileus hemionus columbianus*) under 18 months of age in California more males died than females during winter (Taber and Dasmann 1954). Higher male winter mortality rates documented in the California study conflict with casual observations made by the author during early spring winter–range evaluations in Utah. These impressions indicated exactly the opposite: many more female than male fawns died during winter. Such observations incur greater significance when one considers that males generally predominate in fetal sex ratios (Anderson 1981). If winter mortality among fawns had been random, one would expect to observe more dead male than female fawns. Therefore, this study was initiated to investigate the possible existence of differential winter mortality between mule deer male and female fawns.

Study Area and Methods

The vegetative communities on the study sites were composed of Gambel oak (*Quercus gambelii*), pinyon pine (*Pinus edulis*), Utah juniper (*Juniperus osteosperma*), and big sagebrush (*Artemisia tridentata*) in varying percentages and combinations. Elevation of winter ranges varied from 1500 m to 2300 m. The counties studied were Juab, Salt Lake, Sanpete, Tooele, Utah, and Wasatch. Selected winter ranges in these counties were chosen because of high concentrations of wintering mule deer and past histories of winter losses during winters with higher than average snow fall and subzero temperatures.

Historical data concerning sex ratio of fawns in the study area were taken from Utah Division of Wildlife Resources records on file at the Central Regional Office, Springville, and from a search of the literature. Zwank (1979) completed a study of fawn mortality within the study area and captured 29 male and 22 female fawns (132:100). Additional live-trapping data during the winter on the study area yielded 196 male fawns and 155 females, a sex ratio of 126 male to 100 female fawns (Utah Division of Wildlife Resources records on file in Central Regional Office, Springville). Others working with mule deer fawns in the west show even higher male:female ratios in fetal and neonatal studies (Warren 1973, Papez 1976, Robinette et al. 1957a, 1977, Zeigler 1978, Anderson 1981, Smith 1983). These reported ratios ranged from 101:100 to 172:100 ($N = 4471$, $\bar{X} = 113{:}100$). I used the ratio of 111:100 (Robinette et al. 1957a) in the chi-square statistical analysis. This ratio was used because it represents an average ratio over a number of studies, and this conservative ratio is lower for males than was actually observed in the study area.

Deer winter range in central Utah was searched via horseback during spring 1980 through 1984 in an effort to determine the extent of winter loss of mule deer fawns. Wintering areas were systematically searched at the same intensity (260 km per year) and on predetermined lines of travel each spring. Winter-killed deer were sexed using the presence of antler pedicels to denote male fawns and aged according to the technique described by Robinette et al. (1957b). Records were kept by date, herd unit, sex, age, and drainage. Differential winter mortality of female fawns was tested statistically by chi-square analysis (Huntsberger 1967).

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RESULTS

Mule deer fawn winter loss observed in central Utah, 1980–1984, shows 587 males and 913 females (Table 1). The mean ratio of dead males to females was 100:156 for the study period. The observed winter losses for 1980, 1982, 1983, and 1984, where sample sizes were >200 each year, yielded ratios of 100:159, 100:152, 100:158, and 100:154, respectively.

Chi-square analysis showed that winter mortality of female fawns observed in central Utah was significantly higher ($X^2 = 57.65$, 4df, $P<0.005$) than would be expected from random selection assuming a male to female ratio of 111:100 at birth and equal summer-fall mortality rates (Table 1). The death ratio of male to female fawns showed a range of 100:200–100:152. The five-year mean was 100:156 males to females.

DISCUSSION

Results indicate higher differential winter mortality occurs among female fawns in central Utah. These results differ greatly from the higher male fawn mortality rates reported by Taber and Dasmann (1954) but agree more closely with the 0.94:1.00 male to female ratio found in Utah by Robinette et al. (1957a). He stated, “The winter-loss rate for female fawns is about 1.2 times that of males.”

One possible explanation for the observed differential winter mortality among females and males is that fawn weights recorded in October have shown female fawns to be from 9 to 13% lighter than males (Brown 1961, Austin and Urness 1976, Robinette et al. 1977, Papez 1976, Pederson 1970). During extreme winters, such as those experienced in 1980, 1982, 1983, and 1984, a 9–13% lower body weight for female fawns may be enough of a factor to result in higher winter mortality for females than for males. A realistic maximum allowable weight loss for wild deer is from 20 to 25% of their fall body weight (Brown 1961).

Time of breeding may affect the sex ratio of fawns (Ozoga and Verme 1975). White-tailed deer (*O. virginianus*) females bred early (13–24 hours) in their estrus cycle gave birth to 14.3% male fawns. The percent of male fawns increased up to 80.8 for does bred 49–95 hours after the onset of estrus (Verme and Ozoga 1981). At the start of the breeding season, bucks have more does to service than at the end of the season. Central Utah herds typically have a low buck to doe ratio due to extremely high “buck only” hunting pressure (Jense 1982). For the first estrus cycle of the year, perhaps a higher number of does are bred late in estrus, which results in more male fawns. These would be at least 28 days older than fawns born to does bred in a later estrus cycle; similarly, early-conceived fawns (predominantly female) could be even older. Breeding in the second or third estrus not only results in fawns 28–56 days younger but, because the limited number of bucks have fewer does to service, these offspring may be largely female. Late season (November–December) buck hunts in Utah

TABLE 1. Mule deer fawn winter loss observed in Central Utah, 1980–1983.

Year	Dead male fawns	Dead female fawns	Total dead fawns	Expected number of dead female fawns[1]	Ratio F/M
1980	86	137	223	106	1.59
1981	3	6	9	4	2.00
1982	164	250	414	196	1.52
1983	146	231	377	179	1.58
1984	188	289	477	226	
Total (mean)	587	913	1500	711	(1.56)[*]

[1] Expected number of dead female fawns is calculated by multiplying .474 by the total number of dead fawns. The coefficient .474 is based on the ratio of 111 male fawns to 100 female fawns.

[*] (P<0.005)

may have contributed to disruption of breeding cycles and imbalanced sex ratios in breeding herds. This has profound management implications and should be investigated further. Heavy buck harvest may indirectly be influencing neonatal sex ratios, thus lowering potential winter survival of both sexes of fawns. A large part of the annual fawn crop being born late in the season could result in smaller fawns (of both sexes) entering the winter period. But this may have a greater affect on the female segment of the herd.

The occurrence of differential mortality rates of female fawns is of particular interest because the reproductive segment of the herd is being adversely affected. When such losses occur they must be taken into account by those responsible for drafting management plans and making harvest recommendations. The loss of high numbers of female fawns several years in succession could severely reduce the potential rate of herd increase. A knowledge of the extent of female losses should help managers reduce controllable mortality such as legal harvest.

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LITERATURE CITED

ANDERSON, A. E. 1981. Morphological and physiological characteristics. Pages 27–97 *in* Mule and black-tailed deer of North America, O. C. Wallmo, ed. Univ. of Nebraska Press, Lincoln. 605 pp.

AUSTIN, D. D., AND P. J. URNESS. 1976. Weights of hunter-harvested mule deer in Utah. Utah Science. Utah State Univ. Agric. Expt. Sta. 37(1):11–13.

BROWN, E. R. 1961. The black-tailed deer of western Washington. Washington State Game Dept. Bio. Bull. No. 13. 124 pp.

HUNTSBERGER, D. V. 1967. Elements of statistical inference. 2d ed. Allyn and Bacon. Boston, Massachusetts. 398 pp.

JENSE, G. K. 1982. Utah big game investigations and management recommendation 1981–82. Utah Div. Wildl. Resources Pub. No. 82-3.

OZOGA, J. J., AND L. J. VERME. 1975. Activity patterns of white-tailed deer during estrus. J. Wildl. Manage. 39:679–683.

PAPEZ, N. J. 1976. The Ruby-Butte deer herd. Nevada Dept. of Game and Fish Bio. Bull. No. 5. 61 pp.

PEDERSON, J. C. 1970. Productivity of mule deer on the La Sal and Henry mountains of Utah. Utah Div. of Fish and Game. Pub. No. 70-2. 133 pp.

ROBINETTE, W. L., J. S. GASHWILER, J. B. LOW, AND D. A. JONES. 1957a. Differential mortality by sex and age among mule deer. J. Wildl. Manage. 21:1–16.

ROBINETTE, W. L., D. A. JONES, G. ROGERS, AND J. S. GASHWILER. 1957b. Notes on tooth development and wear for Rocky Mountain mule deer. J. Wildl. Manage. 21:134–153.

ROBINETTE, W. L., N. V. HANCOCK, AND D. A. JONES. 1977. The Oak Creek deer herd in Utah. Utah Div. of Wildl. Resources. Pub. No. 77-15. 148 pp.

SMITH, R. B. 1983. Mule deer reproduction and survival on the La Sal Mountains, Utah. Unpublished thesis. Utah State Univ., Logan. 102 pp.

TABER, R. D., AND R. F. DASMANN. 1954. A sex difference in mortality in young Columbian black-tailed deer. J. Wildl. Manage. 18:309–315.

VERME, L. J., AND J. J. OZOGA. 1981. Sex ratio of white-tailed deer and the estrus cycle. J. Wildl. Manage. 45:710–715.

WARREN, C. P. 1973. Flaming Gorge Reservoir post-impoundment big game study. Utah State Div. of Wildl. Resources. Pub. No. 73-8. 112 pp.

ZEIGLER, D. L. 1978. The Okanogan mule deer. Washington Dept. of Game. Biol. Bull. No. 15. 106 pp.

ZWANK, P. J. 1979. Reduced recruitment in Utah mule deer relative to winter condition. Utah State Div. of Wildl. Resources Pub. No. 79-11. 80 pp.

TRANSVERSE PATTERN OF VEGETATION ON AVALANCHE PATHS IN THE NORTHERN ROCKY MOUNTAINS, MONTANA

George P. Malanson[1] and David R. Butler[1]

ABSTRACT.— The pattern of vegetation on avalanche paths has usually been ascribed to the damage done by snowslides. In the northern Rocky Mountains the pattern of herbs, shrubs, and small trees appears to be more complex than could be accounted for by avalanche magnitude and frequency. The vegetation on one path in Montana illustrates that the topography of the path is a factor in the distribution of species. Three zones exist across avalanche paths: an inner zone of herbs and suffrutescent shrubs occupying a ravine, which is snow covered longer than elsewhere; flanking zones of dense shrubs and trees with flexible stems; and an outer zone of less dense shrubs that is more xeric. The pattern of vegetation seems to be due to avalanche-related stress rather than damage.

Avalanche paths cut vertical swaths through the mature subalpine forests of the western United States. The paths harbor singular assemblages of plant species that are not found elsewhere in the region. Avalanche paths present a variety of ecological problems: they are isolates; they are frequently disturbed; and they contain special features of the physical environment. In this paper we present observations of vegetative patterns on avalanche paths. These observations illustrate that disturbance and stress (sensu Grime 1979) define portions of a continuum of environmental events.

The vegetation on avalanche paths has been discussed in terms of the frequency and magnitude of avalanche events. Ives et al. (1976) described a transverse pattern of tree species on avalanche paths in Colorado. They reported an inner zone of alpine plants or aspen (*Populus tremuloides*) and willow (*Salix* spp.), which they associated with small, frequent avalanches. This inner zone is bounded by a zone of destroyed mature trees with seedlings or saplings of conifers and aspen where avalanches are larger and less frequent. Carrara (1979), also working in Colorado, attributed a similar vegetative pattern to the timing of large and small avalanche events. He distinguished between wider and higher dry snow avalanches and more restricted wet snow slides.

In Washington Smith (1974) attributed the distribution of species on avalanche paths to a combination of avalanche events and moisture gradients. She described a detailed transverse pattern of shrub species. She concluded that the pattern was related to a moisture gradient, which in turn was determined by the frequency of avalanches. Cushman (1976) used multivariate analysis to study avalanche paths in Washington. She found that avalanche frequency could be associated with shrub and tree communities, but was not well associated with herb/shrub communities. She hypothesized that herbaceous species were distributed in response to soil conditions related to snow cover on the paths.

Butler (1979), examining a longitudinal pattern on avalanche paths in Montana, found that flexible-stemmed deciduous trees were more common higher on the paths, and conifers became more common on the less frequently impacted runout zone. He attributed the difference in shrub and herbaceous composition between sites of different aspect (NW/SE) to moisture availability.

On numerous avalanche paths in Montana we have observed that up to three distinct zones occur between the trim lines of the mature forest. Such paths experience a return interval of 3–5 yr (Schaerer 1972, Butler 1979, Butler and Malanson 1984a). An inner zone is dominated by large herbs and suffrutescent shrubs. The inner zone is usually confined to a ravine containing an intermittent stream. On smaller paths the inner zone may be absent. Flanking the inner zone on either side are bands of small deciduous trees and shrubs with flexible stems. The density of shrubs is high in this flanking zone and decreases into the third and outer zone of the path. The outer zone is characterized by a community similar to that of the flanking zone, but at lower density.

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These observations indicate that the transverse patterns of vegetation are more complex than can be accounted for by a magnitude/frequency hypothesis. The following section presents field data describing the transverse pattern of one avalanche path, from which we argue that a hypothesis stating that magnitude and frequency of events directly control the transverse pattern of vegetation on avalanche paths should be rejected.

OBSERVATIONS

SITE.— We chose a single path that has three zones. The path, located on the southern boundary of Glacier National Park, was chosen prior to our perception of the nature of the transverse pattern of the vegetation. It has two source areas at an elevation of about 1800 m. The runout zone, which crosses Shed 7 of the Burlington Northern railroad, is at 1250 m. Tree-ring analysis of conifers damaged by avalanching indicates that major avalanches occurred on this path in 1982, 1979, 1974, 1972, 1970?, 1963, 1957, 1954, 1950?, and 1948 (Butler and Malanson 1984a).

SAMPLE.— With a different purpose in mind, we sampled the vegetation on the path using a forest fire fuel inventory method (Brown et al. 1982). We ran four transects across the path, each 50 m apart. We located a sample plot next to the central stream channel on each transect and at 25 and 50 m away from the stream on both sides. The locations of the sample plots are shown in Figure 1. The topography and the vegetation bands are asymmetrical. Four plots, three on the eastern side of the path, are in the outer zone. The four centrally located plots are in the inner zone. The remaining 12 plots represent the flanking zone.

The fuel inventory for each plot included a count of the deciduous tree or shrub stems in two 1.01 m^2 circular plots. The stems were counted by diameter classes of 0–.5, .5–1.0, 1.0–1.5, 1.5–2.0, 2–3, 3–5, and >5 cm. The percent foliar cover of trees and shrubs in each plot was estimated by two workers, from whose observations a mean was computed. Shrubs and trees were identified by species.

Herbs were sampled by weight only. Four 0.1794 m^2 rectangular plots were arranged at corners of a 2-m square. The plot with the most abundant herb component was selected, and the abundance of the herbs in the other three plots was estimated, by two workers, as a percentage of the first plot. The aboveground herbs from the first plot were then clipped, taken from the field, dried, and weighed. The herbs were not identified by species in these samples, but the presence of dominant herbs was noted.

RESULTS

In the inner zone the plant community is characterized by suffrutescent shrubs and herbs (Table 1). *Heracleum lanatum* is the dominant herb; others include *Veratrum viride* and *Urtica dioica*. The shrub diversity and stem coverage is less than that in the other zones (Table 2). *Rubus parvifolius* is the dominant shrub, although *Cornus stolonifera* and *Populus tremuloides* saplings dominate one inner zone plot. The community of the inner zone occupies a topographic ravine along the stream. At the edge of the ravine the break in slope coincides with a sharp vegetative boundary.

In the flanking zone, shrub and tree species dominate. *Populus tremuloides*, *Acer glabrum*, *Alnus sinuata*, and *Amelanchier alnifolia* are most abundant (Table 2). Shrub diversity is highest in the flanking zone, with richness ranging from 4 to 9. Herb biomass is high, but relatively less important than in the inner zone. On some plots at the left side of the path the herb biomass is notably high

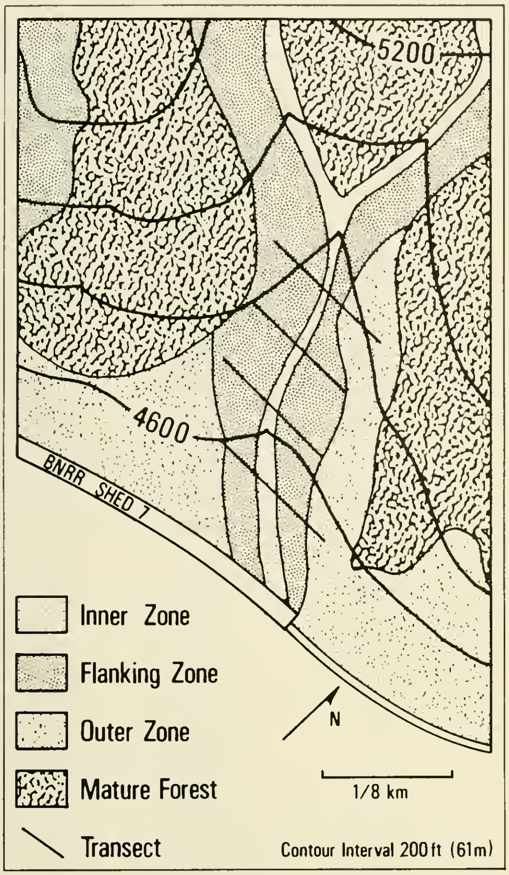

Fig. 1. Map of the vegetative patterns and sample transects on the avalanche path above Shed 7.

where the flanking zone is close to the forest margin (Table 1 and Fig. 1).

In the outer zone on the eastern side of the path shrub diversity, cover and stem density and size are low (Table 2). The biomass of herbs is also relatively low. This zone is comparatively depauperate in both biomass and species richness. It is generally farther from the stream and is open and exposed.

Discussion

The pattern of vegetation we observed could not have resulted from differences in disturbance alone. The vegetation of the inner zone could be damaged by avalanches more frequently than vegetation in the flanking and outer zones; however, the vegetation in these exterior zones is well able to survive avalanche impact and burial. Further, little difference exists in shrub species composition between the flanking and outer zones. The avalanche factor most likely to influence the pattern of vegetation is burial by snow. Avalanches deposit large quantities of snow, even filling the topographic ravines of the inner zone (Butler 1984). The inner zone may remain under snow for several weeks after the rest of the path is clear. This shorter growing season is a stress (sensu Grime 1979), not a disturbance; growth is slowed, not destroyed. The primary factor is therefore topographic, not catastrophic.

From the edge of the inner ravine to the trimline of the path, a moisture gradient probably exists. The shrubs near the ravine should have access to a larger supply of soil moisture from the melting snow in the ravine and, later in the year, from the water table. The outer zone would have less accessible water, and, because it is more open, a more xeric microclimate. These views on available soil moisture are, at this time, necessarily speculative, but the differences in microclimate are obvious.

As noted above, some narrower avalanche paths lack a distinct inner zone. With less snow and less water, a deep ravine does not develop; the pattern of snow cover does not exist; and shrubs and trees are able to occupy the center of the path. In casual observations

Table 1. Biomass and foliar cover of herbs and shrubs on the plots in the inner (I), flanking (F), and outer (O) zones.

		Biomass (kg/m²)		Cover (%)	
Plot	Zone	Herbs	Shrubs	Herbs	Shrubs
1	O	0.0250	0.5448	8	16
2	F	0.0773	9.4272	50	79
3	I	0.0463	1.5421	8	84
4	F	0.0477	8.4414	40	88
5	O	0.1065	0.8652	70	50
6	F	0.0584	12.4199	13	88
7	F	0.0522	10.1310	32	69
8	I	0.0820	4.6126	40	79
9	F	0.1194	3.0455	13	98
10	F	1.8729	0.8468	60	50
11	F	0.1071	8.4989	22	50
12	F	0.1023	0.8256	50	60
13	I	0.0923	1.1341	42	60
14	F	1.0080	7.3870	84	64
15	F	0.3463	2.1637	32	79
16	O	0.0777	0.4371	8	40
17	O	0.1384	0.7979	60	22
18	I	0.1260	0.4959	93	50
19	F	0.4817	1.2783	74	60
20	F	0.0687	9.6440	16	79

TABLE 2. Shrub stem area, stem density, and basal areas of the plots.

Plot	Species	Mean stem area (cm^2)	Stems/ Ha	Basal area/ Ha
1	*Amelanchier alnifolia*	.22	79,229	17,431
	Berberis repens	.14	44,567	6,175
2	*Amelanchier alnifolia*	.47	128,748	59,953
	Berberis repens	.05	24,759	1,238
	Populus tremuloides	7.50	14,856	11,402
	Prunus virginiana	.09	44,567	3,812
	Rosa spp.	.05	19,808	973
	Rubus idaeus	.05	34,663	1,702
	Vaccinium scoparium	.10	74,278	7,147
3	*Alnus sinuata*	.05	4,952	243
	Cornus stolonifera	.24	44,567	10,483
	Ribes lacustre	.20	9,904	1,945
	Rosa spp.	.36	34,663	12,589
	Rubus parviflorus	.44	14,856	6,563
	Vaccinium scoparium	.33	24,759	8,216
4	*Amelanchier alnifolia*	.44	4,952	2,188
	Populus tremuloides	9.62	14,856	142,927
	Prunus virginiana	.44	4,952	2,188
	Rhamnus alnifolia	.12	69,326	8,282
	Rosa spp.	.05	4,952	243
	Rubus parviflorus	.44	14,856	6,563
	Sorbus scopulina	2.90	14,856	43,011
	Vaccinium scoparium	.15	69,326	10,068
5	*Amelanchier alnifolia*	.61	19,808	12,047
	Berberis repens	.20	69,326	13,612
	Prunus virginiana	.51	44,567	22,587
	Rhamnus alnifolia	.79	9,904	7,779
	Rosa spp.	.05	4,952	243
	Rubus idaeus	.05	19,808	973
	Vaccinium scoparium	.14	29,711	4,117
6	*Arctostaphylos uva-ursi*	.05	9,901	486
	Berberis repens	.05	4,952	243
	Rubus ideaus	.05	44,567	2,188
	Rubus parviflorus	.05	4,952	243
	Spirea betulifolia	.34	138,651	47,435
	Vaccinium scoparium	.05	24,759	1,216
7	*Ceanothus* spp.	2.41	4,952	11,911
	Populus tremuloides	38.48	4,952	190,569
	Prunus virginiana	2.01	24,759	49,781
	Rosa spp.	.44	4,952	2,188
	Spirea betulifolia	.05	9,901	486
	Vaccinium scoparium	.44	19,808	8,751
8	*Cornus stolonifera*	.52	39,615	20,414
	Loncifera involuctra	1.00	19,808	19,864
	Populus tremuloides	2.24	19,808	44,431
	Rubus idaeus	.05	4,952	243
	Rubus parviflorus	.44	34,663	15,314
	Salix spp.	1.23	9,904	12,154
9	*Amelanchier alnifolia*	1.23	4,952	6,077
	Cornus stolonifera	1.43	24,759	35,440
	Rubus parviflorus	.24	24,759	5,883
	Sorbus scopulina	.88	9,904	8,740
	Vaccinium globulare	.28	99,037	28,002
10	*Amelanchier alnifolia*	.05	9,904	486
	Berberis repens	.05	4,952	243
	Prunus virginiana	.10	24,759	2,382
	Rosa spp.	.17	34,663	5,761
	Rubus parviflorus	.23	59,422	13,609
	Vaccinium globulare	.25	89,133	21,954

Table 2 continued.

Plot	Species	Mean stem area (cm^2)	Stems/ Ha	Basal area/ Ha
11	*Acer glabrum*	.08	123,796	9,344
	Amelanchier alnifolia	.49	54,470	26,700
	Arctostaphylos uva-ursi	.05	14,856	729
	Berberis repens	.05	9,904	486
	Populus tremuloides	3.98	24,759	98,444
	Prunus virginiana	.08	34,663	2,788
	Rubus idaeus	.05	118,844	5,834
	Vaccinium globulare	.05	4,952	243
	Vaccinium scoparium	.05	4,952	243
12	*Amelanchier alnifolia*	.26	44,567	11,775
	Pachistima myrsinites	.05	39,615	1,945
	Populus tremuloides	.44	4,952	2,188
	Prunus virginiana	.44	4,952	2,188
	Rosa spp.	.44	9,904	4,376
	Rubus idaeus	.05	99,037	4,862
	Spirea betulifolia	.14	29,711	4,117
	Vaccinium scoparium	.07	49,518	3,500
13	*Rubus parviflorus*	.29	183,219	53,545
14	*Acer glabrum*	2.81	44,567	125,032
	Amelanchier alnifolia	.28	49,518	14,001
	Berberis repens	.05	9,904	486
	Pachistima myrsinites	.05	4,952	243
	Rubus parviflorus	.24	24,759	5,883
	Spirea betulifolia	.08	44,567	3,364
15	*Acer glabrum*	.40	34,663	13,724
	Amelanchier alnifolia	1.23	9,904	12,154
	Pachistima myrsinites	.08	34,663	2,788
	Rubus parviflorus	.44	34,663	15,314
	Spirea betulifolia	.05	24,759	1,216
	Vaccinium globulare	.15	79,229	12,047
	Vaccinium scoparium	.26	44,567	11,775
16	*Amelanchier alnifolia*	.10	49,518	4,764
	Arctostaphylos uva-ursi	.06	128,748	7,372
	Berberis repens	.05	49,518	2,431
	Rubus idaeus	.05	49,518	2,431
	Vaccinium scoparium	.03	99,037	2,697
17	*Amelanchier alnifolia*	.41	79,229	32,258
	Berberis repens	.05	44,567	2,188
	Rosa spp.	.05	24,759	1,216
	Rubus idaeus	.05	69,326	3,403
	Vaccinium scoparium	.08	39,615	2,990
18	*Prunus virginiana*	.14	14,856	2,058
	Rosa spp.	.20	9,904	1,945
	Rubus parviflorus	.17	34,663	5,761
	Unidentified	.44	14,856	6,563
	Vaccinium scoparium	.29	54,470	14,919
19	*Amelanchier alnifolia*	.36	99,037	35,967
	Pachistima myrsinites	.10	99,037	9,529
	Rubus idaeus	.05	14,856	729
	Vaccinium scoparium	.20	9,904	1,945
20	*Alnus sinuata*	3.53	59,422	209,753
	Amelanchier alnifolia	.64	49,518	31,502
	Pachistima myrsinites	.11	19,808	2,247
	Rubus idaeus	.05	19,808	973
	Rubus parviflorus	.11	19,808	2,247
	Spirea betulifolia	.05	29,711	1,459
	Vaccinium globulare	.20	19,808	3,889

we detected considerable variation in the shapes and widths of the patterns. Although our data illustrate only one case, the topography of the paths seems more important than avalanche source areas in affecting the patterns.

Two areas of ecology have been separated in the recent literature: stress and disturbance (Cairns 1980, Barrett and Rosenberg 1981). We believe that, although some adaptations seem to be selected by either stress or disturbance, many environmental events have an effect that varies between stress and disturbance. The effect may depend on the intensity of the event. Following the definitions of stress and disturbance of Grime (1979), an event such as flooding may stress some species and damage others. Different flood events could damage all species or only stress all species (cf Malanson and Kay 1980, Menges and Waller 1983). Avalanche events also vary in intensity. The avalanches of Glacier National Park, Montana, and of the Cascades, Washington, are more often wet snowslides with lower velocities and impact pressures than would be found in the dry snow avalanches of Colorado and Utah. This difference may account for the simpler pattern described by Ives et al. (1976). Carrara (1979) thought that the pattern he observed was due to an older dry snow avalanche affecting the entire path, and a recent wet snow avalanche affecting only the inner zone. The difference in the location of wet and dry slides within a path may be of importance in Montana also (Butler and Malanson 1984b). In general, stress and disturbance in plant ecology can and should be integrated through an analysis of the environmental events.

Acknowledgments

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Literature Cited

Barrett, G. W., and R. Rosenberg, eds. 1981. Stress effect on natural ecosystems. Wiley, Chichester.

Brown, J. K., R. D. Oberheu, and C. M. Johnston. 1982. Handbook for inventorying surface fuels and biomass in the interior west. U.S. For. Serv. Gen. Tech. Rep. INT-129.

Butler, D. R. 1979. Snow avalanche path terrain and vegetation, Glacier National Park, Montana. Arct. Alp. Res. 11:17–32.

———. 1984. Vegetative and geomorphic change on subalpine snow avalanche paths, Glacier National Park, Montana, USA. Submitted to Earth Surface Processes & Landforms.

Butler, D. R., and G. P. Malanson. 1984a. A history of high-magnitude snow avalanches, southern Glacier National Park, Montana, USA. Mountain Res. & Dev. In press.

———. 1984b. A reconstruction of snow avalanche characteristics in Montana, USA, using vegetative indicators. Submitted to J. Glaciology.

Cairns, J., ed. 1980. The recovery process in damaged ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Carrara, P. E. 1979. The determination of snow avalanche frequency through tree-ring analysis and historical records at Ophir, Colorado. Geological Society of America Bulletin 90:773–780.

Cushman, M. J. 1976. Vegetation composition as a predictor of major avalanche cycles, North Cascades, Washington. Unpublished thesis. Univ. of Washington, Seattle.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, Chichester.

Ives, J. D., A. I. Mears, P. E. Carrara, and M. J. Bovis. 1976. Natural hazards in mountain Colorado. Ann. Assoc. Amer. Geogr. 66:129–144.

Malanson, G. P., and J. Kay. 1980. Flood frequency and the assemblage of dispersal types in hanging gardens of the Narrows, Zion National Park, Utah. Great Basin Nat. 40:365–371.

Menges, E. S., and P. M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. Amer. Nat. 122:454–473.

Schaerer, P. A. 1972. Terrain and vegetation of snow avalanche sites at Rogers Pass, British Columbia. Pages 215–222 *in* O. Slaymaker and H. J. McPherson, eds., Mountain geomorphology. Tantalus, Vancouver.

Smith, L. 1974. Indication of snow avalanche periodicity through interpretation of vegetation patterns in the North Cascades, Washington. Unpublished thesis. Univ. of Washington, Seattle.

EFFECTS OF 2,4-D ON A *POPULUS TREMULOIDES* COMMUNITY IN THE WESTERN UNITED STATES—22 YEARS AFTER TREATMENT

Dale L. Bartos[1] and James E. Lester[2]

Abstract.— Quaking aspen (*Populus tremuloides* Michx.) stands were accidentally sprayed with 2,4-D in a sagebrush control program in western Wyoming in 1958. We visited the site during the summer of 1981 to evaluate the long-term effect on the aspen trees and the associated vegetation. Initially, some observers believed that the aspen had been "destroyed." Subsequent data indicate just the opposite—aspen stocking appeared to have been improved by the treatment. On two of the sampled clones, 22 years after spraying, there were approximately 17,000 more suckers/ha on the sprayed than on the unsprayed plots. These are adequate numbers to restock the site to pretreatment densities. Although undergrowth vegetation appeared to be changed as a result of the treatment, this cannot be attributed solely to the herbicide because heavy grazing, mostly by domestic livestock, has occurred on the grazing allotment. A similarity index was calculated between sprayed and unsprayed portions of the same aspen clones. Forbs were still less on the sprayed areas, whereas grasses were similar on the sprayed and unsprayed areas. Spraying apparently does not have as adverse an effect on aspen communities as some conservationists originally thought.

The aspen (*Populus tremuloides* Michx.) ecosystem, widespread throughout North America (Little 1971), is a major forest type in the Rocky Mountains. This system produces multiple resources including wildlife habitat, wood fiber, and summer grazing for domestic livestock.

Through the process of natural plant succession many aspen forests in the West are succeeding to either conifer- or shrub-dominated communities. Such conversions are a concern to the resource manager because valuable forage and wildlife habitat is lost in the process.

Understanding the role of disturbance (e.g., herbicides) as a tool for altering succession in the aspen ecosystem will contribute toward our understanding the functioning of the system and serve as a basis for developing sound management alternatives. The two most practical management alternatives for aspen lands at present are: (1) permit aspen-to-conifer succession to proceed in seral communities, or (2) manipulate the system (i.e., burning, cutting, spraying) to set back plant succession and perpetuate aspen communities. Usually, both of these alternatives are imposed in conjunction with grazing pressure from domestic livestock. Such perturbations and subsequent plant succession causes changes in resource values and other alterations in the ecosystem. The short- and long-term responses must be quantified, where possible, to serve as the basis for sound land management decisions.

Although spraying of herbicides is a means of manipulating the aspen system, it has seldom been used in the western United States because of anticipated "adverse" environmental consequences. This study sought information from an aspen site that was accidentally sprayed with herbicides, and it should give us a better understanding of the system's response to such disturbance. This knowledge should result in more meaningful management recommendations and will serve as a basis for developing future studies on proposed spray sites in the Bridger-Teton (Wyoming) and Caribou (Idaho) national forests.

In 1958, an extensive spraying operation to control sagebrush was carried out on the Mosquito Lake Unit of the Upper Green River Allotment, Bridger National Forest, in western Wyoming. Approximately 3640 ha of big sagebrush (*Artemisia tridentata* Nutt.) was treated by aerial application of low volatile 2,4-D ester. With respect to range improvement, the project was deemed a total success (Lester 1972). However, large tracts of quaking aspen and a few conifers were killed or injured during the operation. The Forest Service's sagebrush control program then fell under severe criticism by many conservationists, including Justice of the Supreme Court William O. Douglas. At the time, the Forest Service's sagebrush-spraying operation was curtailed on the Upper Green River Allotment and the region reassessed its methodology and changed from fixed-wing to helicopters for applications of herbicides (William F. Davis, pers. comm.).

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Only one other report of the use of phenoxy herbicides on aspen in the Intermountain West was found. This was a Forest Service administrative study done by the Fishlake National Forest in central Utah. Between 1965 and 1967, 190 ha were repeatedly sprayed (up to 6 times during the growing season) in an attempt to convert the deep-rooted aspen and associated communities to a more shallow-rooted grass type to increase water production (Robinson 1971). Aspen were virtually eliminated from the site and grass production increased approximately 10 times. However, other problems arose as a result of the elimination of forest cover, including mass slumping, accelerated erosion, and some damage to wildlife habitat. Robinson (1971) further indicated that "massive applications of herbicides to aspen and associated plant communities are not recommended at present since the full ecological impact of such treatment is not known."

The accidentally sprayed site in western Wyoming offered an excellent opportunity to monitor the response of aspen to herbicides. Although 22 years have elapsed since the spraying occurred, useful information is still available because of the reproductive strategies of aspen. Generally, aspen reproduces profusely by root suckers after a disturbance. Current levels of aspen reproduction should indicate the degree of "damage" the aspen actually did sustain. These data will be particularly useful now because of the renewed interest in using herbicides to manipulate aspen forests, especially on lands not conducive to treatment by burning or cutting.

The two main objectives of this study were:

1. To determine the suckering response of aspen in the sprayed clones. Sucker density should be an adequate indicator of the ability of the clone to regenerate after disturbance. Measuring the juvenile individuals should give us a better understanding as to whether or not the aspen on the site were "destroyed" by this accidental spraying operation.

2. To determine the long-term change in undergrowth. Initial changes in the undergrowth vegetation are not available. However, long-term differences can be assessed by comparing sprayed and unsprayed portions of the same clones. If such differences are still detected in the understory vegetation, this could indicate where the successional process is in returning the site to pretreatment conditions.

STUDY AREA

The Mosquito Lake Grazing Unit, at the north end of the Bridger National Forest, is presently administered as part of the Bridger-Teton National Forest (Fig. 1). The unit is approximately 56 km north of Cora, Wyoming, in the northwest part of the state. The 5261 ha grazing unit is subdivided into four pastures. Geographically, the study site lies in several sections of Townships 39 and 40 North, range 110 West, at an elevation of approximately 2760 m. The climate consists of short, cool summers and long, severe winters, with average yearly precipitation of about 46 cm (Lester 1972).

The Mosquito Lake Grazing Unit is a high mountain grassland with adjacent woody communities. In the south central portion of the unit the open grasslands are interspersed with shrubby and woody vegetation. Aspen is the dominant woody species with an understory consisting of species such as bush cinquefoil (*Potentilla fruticosa* L.), mountain snowberry (*Symphoricarpos oreophilus* Gray), and bearberry (*Arctostaphylos uva-ursi* [L.] Spreng.). A few small lodgepole pine (*Pinus contorta* Dougl.) also occur. Reed (1971) designated this type as a *Populus tremuloides*/*Symphoricarpos oreophilus* association.

METHODS

Sampling was limited to those areas that had aspen. Aspen clones were selected that

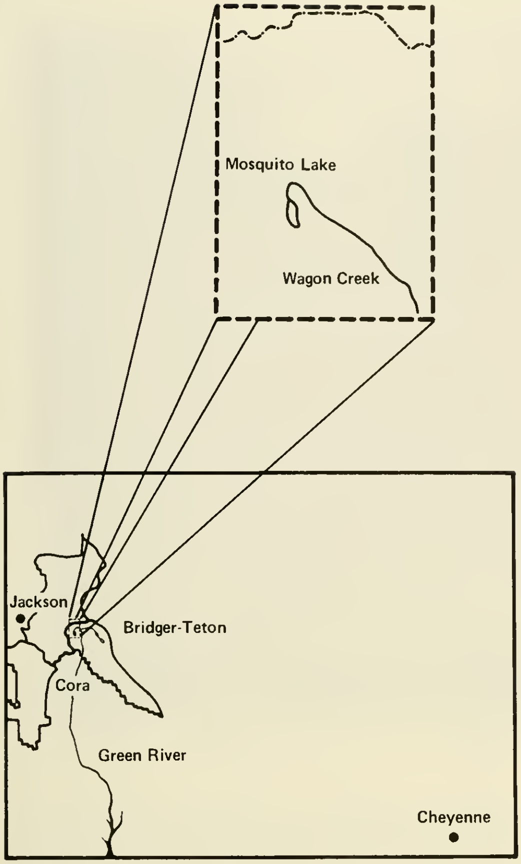

Fig. 1. Map of the Mosquito Lake study area in relation to the Green River system in Wyoming.

appeared to have been on the edge of the sprayed area, resulting in one portion of the clone having been treated with herbicides and the other portion missed. Thus, treated and untreated (control) plots were selected from a single clone. Three aspen clones were located that met the above criteria, and six sampling plots were established within these clones.

The selected clones apparently occupied different sites both because of site physiography and the differences observed in the undergrowth vegetation. Site 1 would probably be classified as POTR/BERE c.t., site 2 is clearly a POTR/SYOR c.t., and site 3 is a POTR/ARTR c.t. (Youngblood and Mueggler 1981).

Aspen suckers were counted on three transects per treatment and classified as to current year or older. These transects were 30 m long and 2 m wide and were selectively located so they would fall within the clone. Suckers were categorized as follows: < 0.5 m tall, 0.5–2 m tall, and > 2 m tall and < 5.1 cm diameter at breast height (dbh). Three representative suckers per height class were cut and aged. Also, conifer reproduction was noted.

To characterize the aspen clones, plots that were 100 m^2 (10 x 10 m) in size were established. Within these plots, all mature trees (>5.1 cm dbh) were tallied, and height, dbh, and age were measured using standard techniques for five of the largest trees.

Undergrowth production was measured at or near its peak during the first week of August 1981. Total production was obtained and expressed on a dry weight basis. Measurements were made using three sets of five, 0.5 m^2 circular quadrats that were randomly distributed within the 100 m^2 macroplot in each treatment. The current year's biomass was estimated on each of four quadrats as a percent of the fifth one. The reference quadrat (fifth) was clipped of all vegetation to ground level, dried in an oven at 70 C till it reached a constant weight (at least 48 hours), and weighed. The percentage estimates were converted to weights and the average weights of the 15 quadrats were expressed as kilograms dry weight per hectare. When sampled, the pasture was being grazed by cattle, so total production figures are lower than they would have been under nongrazing conditions.

The four pastures in the grazing unit are managed in a rest-rotation system—each pasture is grazed for three years and rested one. Comparison of the sampled pasture to the rested pasture allowed us to estimate use as approximately 75%. Grazing, however, appeared to be uniform across each clone sampled.

A list of all major plant species was developed from observations made within the 100 m^2 plot. The following cover class assignments were used to quantify various species and species groups on the plot:

Class	*Percent*
1 =	Trace–1
2 =	1–5
3 =	5–15
4 =	15–25
5 =	25–50
6 =	50–100

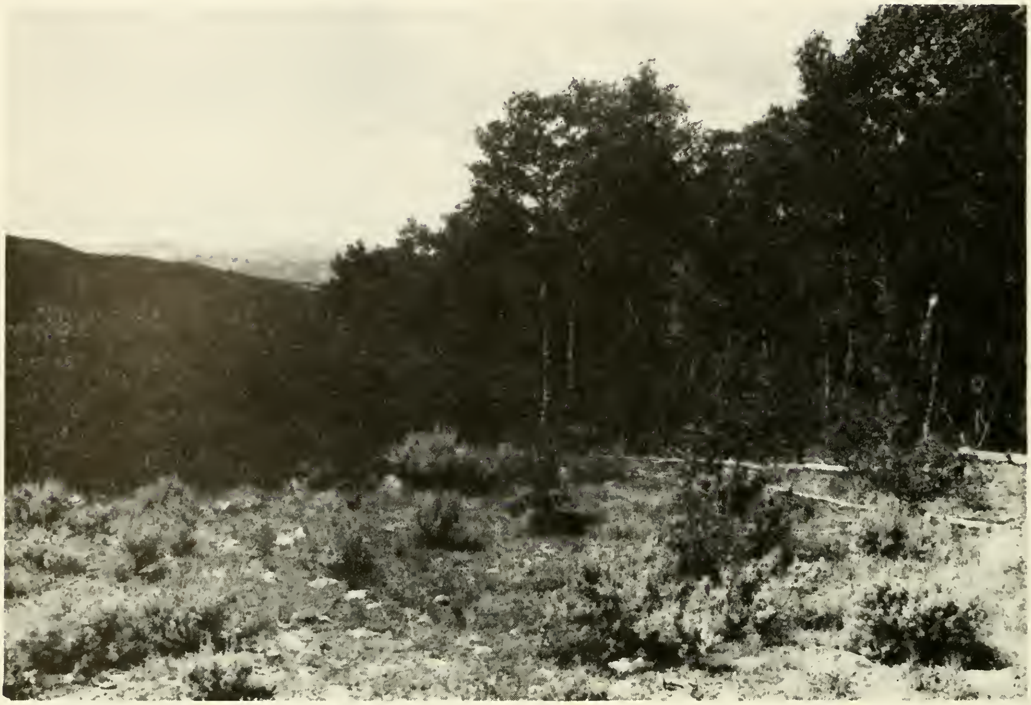

Fig. 2. General views of the three study sites: A, site 1. B, site 2. C, site 3 (next page). Note the sharp contrast between the sprayed and unsprayed portion of each clone.

Results and Discussion

Aspen Trees

The aspen responded to spraying essentially as we had anticipated. The aboveground portion of the overstory trees was almost totally killed by the accidental application of 2,4-D, and there was a release of aspen suckers. But these findings need to be put in proper perspective: all measurements were made 22 years after the site was treated, and no initial or intermediate sampling was carried out on the aspen sites. However, the junior author worked on the sagebrush-grassland portion of this grazing allotment 10 years after treatment and observed that considerable damage had been done to the aspen. He (1972) stated that "large tracts of quaking aspen and a small number of conifers were eliminated or injured during the operation."

A distinct difference was observed between the sprayed and unsprayed portion of the clones sampled (Fig. 2). After 22 years, we found essentially no mature trees on the sprayed portion of the clones. We did encounter one tree in the 10.2 to 15.2 cm category on one of the transects in site 2. On the same site we found almost 600 suckers/ha that were larger than our biggest reproduction category, e.g., greater than 5.1 cm dbh and more than 2 m tall. We assumed these individuals were not more than 22 years old. We thus concluded that most of the aboveground portion of the trees and reproduction were completely killed by the herbicide and all died shortly after application. The unsprayed portion of the clones were considered to represent pretreatment conditions. The stands measured were multistoried (Table 1) and ranged in density from 1600 to 3700 trees/ha. These densities are equal to or more than double those reported by Schier (1975) for 80-year-old, healthy clones in northern Utah.

No distinct patterns emerged from the descriptive data obtained from the five largest trees in each clone (Table 1). However, the aspen trees on site 2 are shorter, smaller in diameter, and have less basal area even though these trees are not the youngest of the three sites. According to Baker's (1925) classi-

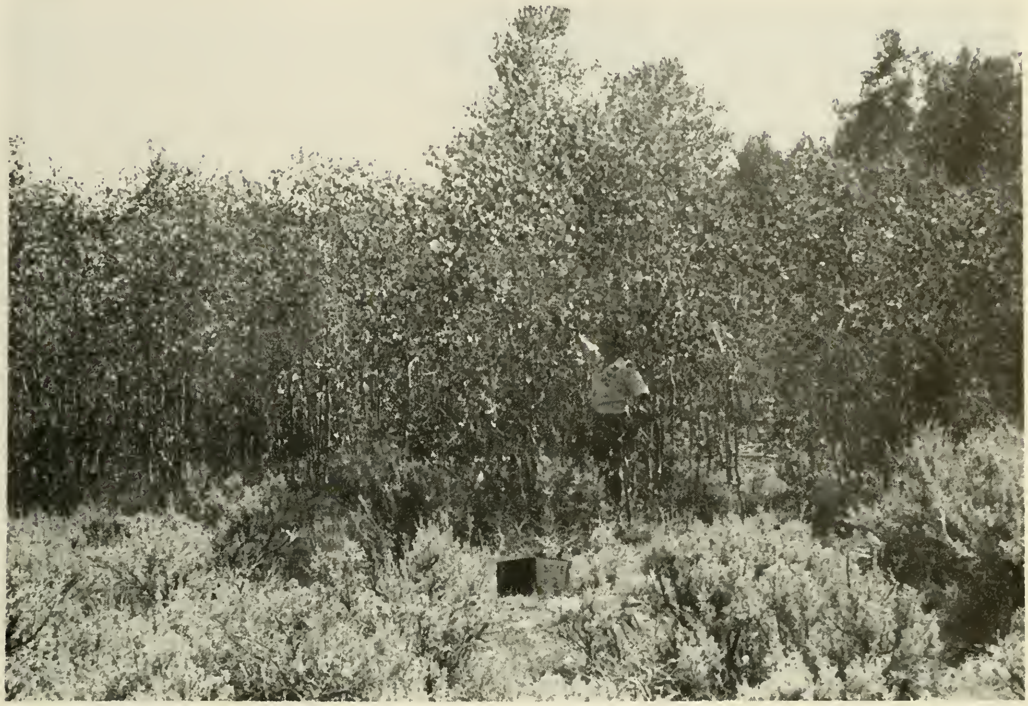

Fig. 2 continued: C, site 3.

fication, the site quality would be site IV for all three areas, which is a poor site with little chance of producing aspen wood products other than firewood.

The basal areas calculated for the three sampled clones appear to be large when compared with other western aspen sites (Baker 1925, Jones and Trujillo 1975, Schier 1975, and Harniss and Harper 1982). However, our values lie at the upper end of the range reported by Mueggler and Campbell (1982) for aspen forests in southern Idaho.

Table 1. Stand values for density, diameter at breast height (dbh), and basal area of mature aspen trees and height and age of the five largest aspen trees on the unsprayed plots for three sites.

	Numbers/ha		
Values	Site 1	Site 2	Site 3
Density			
5.1–10.2 cm	1,000	1,200	—
10.3–15.2 cm	1,300	1,500	300
15.3–20.3 cm	600	1,000	600
20.4–25.4 cm	400	—	400
25.5–30.5 cm	100	—	300
Total	3,400	3,700	1,600
dbh (cm)	13.8	12.5	20.0
Basal area (m^2/ha)	58.7	49.5	53.7
Ht (m)	10.6	8.9	14.1
Age (years)*	54.0	56.3	82.8

*Base of tree was used to determine age.

Aspen Suckers

After 22 years, there were still sufficient numbers of aspen suckers (Table 2) to restore the sites to densities that existed prior to treatment. In 1981, there were between 18,000 and 24,000 suckers/ha on the sprayed sites and between 3,000 and 20,000 on the unsprayed areas. Only site 1 had no significant statistical differences between the number of suckers on the treated and the un treated portion of the clones. Such reproduction on the control plots would indicate that the three clones were self-regenerating.

Disturbances (burning or cutting) of the aspen forest in the West can result in sucker densities of between 5,000 and 45,000/ha (Jones and Trujillo 1975). Generally, the number of suckers peak the first year after disturbance (Sampson 1919, Baker 1925, Smith et al. 1972, Jones 1975) and then decline over several years until the numbers stabilize at a level comparable to what was

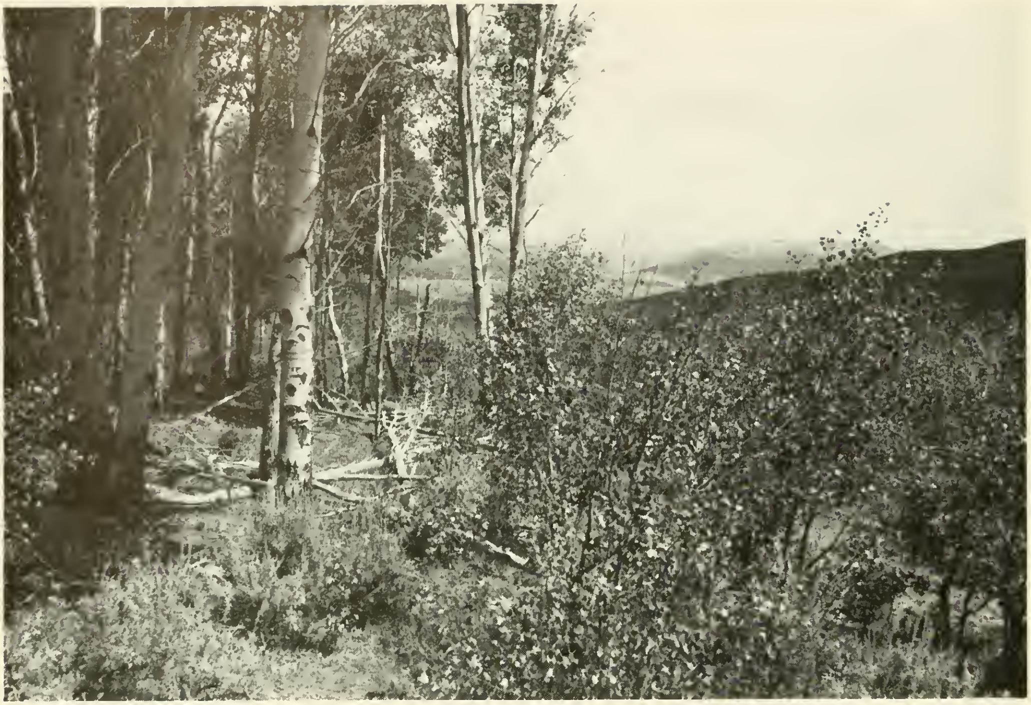

Fig. 2 continued: C, site 3.

on the site before treatment. The aspen regeneration at the Mosquito Lake study area had not stabilized at pretreatment densities after 22 growing seasons. This lack of stability can be attributed in part to use by both domestic livestock and wildlife. Jones (1976) has indicated that 50,000 to 75,000 suckers/ha in the first year after disturbance is not excessive because of the natural thinning that occurs in aspen stands. The suckers had probably peaked at a higher number and have since declined to the numbers observed.

The tremendous suckering ability of western aspen has been substantiated by several studies. Mueggler and Bartos (1977) and Bartos and Mueggler (1982) reported 20-fold increases in sucker numbers (up to 50,000/ha) in both southern and northern Utah after aspen had been clearcut. On another northern Utah site that was cut, Smith et al. (1972) de-

TABLE 2. Current year aspen suckers and those two years old and older presented for three size classes. Also given are the mean ages for the various size suckers.

	Current suckers	<0.5 m tall suckers		0.5–2 m tall suckers		>2 m tall and < 5.18 cm dbh		Total number of suckers,
Site	Numbers/ha	Numbers/ha	Years	Numbers/ha	Years	Numbers/ha	Years	Numbers/ha
SITE 1								
Sprayed	889	4,278	5	7,389	9	6,222	19	18,778
Unsprayed	1,278	10,611°	5	6,389	10	1,389°	14°	19,667
SITE 2								
Sprayed	444	7,556	4	3,444	8	12,278	17	23,722
Unsprayed	333	4,611°	5	889°	14	278°	18	6,111°
SITE 3								
Sprayed	111	5,444	4	5,611	9	8,167	15	19,333
Unsprayed	278	1,944°	8	389°	11	56°	12	2,667°

°Statistical difference between the sprayed and control plots (P>.90).

termined there were between 74,000 and 124,000 suckers/ha. Jones (1975) found 35,000 suckers/ha on aspen clearcuts in Arizona. In southwestern Colorado Hittenrauch (1976) reported from 15,000 to 25,000 suckers/ha.

The aspen suckers varied in age from 1 year (current) to 22 years. Within the constraints of our limited sample size and because no suckers were found to be over 22 years old, we assume that virtually all the pretreatment reproduction was killed in the spraying operation. Drift from the herbicide application might even have affected the unsprayed portions of the sites. However, it is more likely that other factors (e.g., animal use, suppression by mature trees) are responsible for the absence of suckers older than 22 years. No conifer reproduction was found on our transects, although some lodgepole pine seedlings were observed within the clones.

Undergrowth Production

Although undergrowth production was determined at peak growth, grazing by domestic livestock was intense in this pasture during the summer of 1981. Production values, therefore, are distorted and are at least 75% below actual production.

Table 3 shows the measured undergrowth production for the three aspen clones. On all three sites there were significant differences in standing herbage between the sprayed and unsprayed portion. The sprayed areas on both sites 2 and 3 had approximately twice the undergrowth as their respective control areas. It was just the opposite on site 1. These inconsistencies do not appear related to environmental or edaphic factors. A strong positive relationship exists between sucker numbers and undergrowth production on the unsprayed portions of the three clones. This increase in production can be attributed to the aspen reproduction restricting use by animals. No clear pattern emerges to indicate whether or not spraying has a detrimental effect on undergrowth production.

The aspen understory communities in this area have been designated by Reed (1971) as a POTR/SYOR association, and the community types for the three sites are POTR/BERE (site 1), POTR/SYOR (site 2), and POTR/ARTR (site 3), according to Youngblood and Mueggler (1981).

Youngblood and Mueggler found undergrowth production values to vary between 800 and 1500 kg/ha; however, they made no reference to the amount of grazing they encountered. Our values are somewhat comparable to theirs, particularly when one considers that approximately 75% of the production had been utilized.

Species Composition

Composition of the undergrowth in these aspen forests was only moderately complex. Only 15 species of plants were sufficiently abundant to individually constitute at least 1% of the undergrowth production on any of the study sites.

In general, it is difficult to say whether spraying changed the species composition. No general trends are readily obvious, but this could be attributed in part to the extensive grazing on these sites during the 1981 grazing season and in previous years. More forbs were found on the unsprayed plots than on the sprayed areas, which agrees with observations made in Canada by Hilton and Bailey (1974), who found increases in grass and grasslike species, and by Bowes (1978), who reported forbs were reduced as a result of spraying.

The only two forbs that occurred on all sampled sites were sticky geranium (*Geranium viscosissimum* F. & M.) and Nuttall aster (*Aster perelegans* Nels. & Macbr.). The geranium was the most abundant. Other important forbs that contributed to the overall makeup were showy frasera (*Frasera speciosa* Dougl.), strawberry (*Fragaria vesca* L.), and northern sweetvetch (*Hedysarum boreale* Nutt.). The proportion of graminoids in the undergrowth varied from a trace to 20%.

Table 3. Peak herbage present on plots in heavily grazed aspen clones on the Upper Green River Allotment.

	Kg/ha		
	Sprayed		Unsprayed
Site 1	446.4	*	767.4
Site 2	481.8	*	260.4
Site 3	577.5	*	294.9

*Statistical difference between the sprayed and control plots ($P > .999$).

Slender wheatgrass (*Agropyron caninum* [L.] Beauv.), sedge (*Carex* spp. L.), Idaho fescue (*Festuca idahoensis* Elmer), and Letterman needlegrass (*Stipa lettermani* Vasey) were most abundant. Letterman needlegrass contributed most to the graminoids overall and in particular on the sprayed plots. No consistent trends were observed in the shrubs encountered. Big sagebrush, woods rose (*Rosa woodsii* Lindl.), and mountain snowberry were by far the most abundant shrubs. The target species in the spraying operation was big sagebrush, which was abundant on two of the sprayed portions of the sites. This abundance might indicate that sagebrush is not as susceptible to 2,4-D when it occurs under an aspen canopy.

To facilitate understanding the overall divergence of undergrowth composition caused by spraying, we computed Sorensen's community coefficient (Mueller-Dombois and Ellenberg 1974) as an index to the similarity between sprayed and unsprayed plots. The data used in this comparison were percentage composition based on cover of the undergrowth species rather than actual production. Thus, the index compares proportions of species irrespective of differences in total undergrowth production. Aspen reproduction was excluded from the analysis. An index value of 1.00 indicates identical matching of species and composition on the compared areas. A value of 0.00 would indicate that the areas have no species in common.

When all species were used, the similarity index (S.I.) between the sprayed and unsprayed plots for sites 1, 2, and 3 was 0.24, 0.50, and 0.34, respectively. Because after 22 years these values indicate dissimilarity in species composition on the treated and control plots for the three sites, it will probably be a considerable length of time before these areas return to their pretreatment similarity. An S.I. was also calculated for forbs, shrubs (minus aspen reproduction), and grasses on the treated and untreated portion of the clones. Extremes in S.I. were found in the shrub category with 0.08 on site 2 and 0.78 on site 1. Higher S.I. were found for grass and grasslike species (site 1 = 0.19, site 2 = 0.68, and site 3 = 0.57) than for forbs (site 1 = 0.40, site 2 = 0.31, and site 3 = 0.24). These results substantiate that grasses are not harmed appreciably, but forbs are harmed by 2,4-D.

Conclusions

The accidental spraying of aspen that occurred on the Upper Green River grazing allotment appeared to be an excellent opportunity to evaluate the long-term effects of herbicides on the aspen system. Although the treatment occurred 22 years before, we decided that valuable information could still be gathered because of the growth response of aspen. We found that the aboveground portion of the aspen trees and reproduction was almost totally killed as a result of the single spraying with 2,4-D. Sprayed areas had approximately 20,000 suckers/ha, which for two of the three sites sampled was almost six times more than the tree densities on the control plots. Treatment by herbicides appears to have aided the aspen by promoting suckering.

Undergrowth production under heavy grazing was low, with approximately 500 kg/ha being recorded. The shrub and forb component appeared to be most adversely affected by the treatment, but the graminoids were somewhat favored.

Literature Cited

Baker, F. S. 1925. Aspen in the central Rocky Mountain region. U.S. Dept. Agric. Bull. 1291. 46 pp.

Bartos, D. L., and W. F. Mueggler. 1982. Early succession following clearcutting of aspen communities in northern Utah. J. Range Manage. 35(6):764–768.

Bowes, G. G. 1978. Advantages of herbicides for brush control on newly seeded rangeland in western Canada. Pages 651–653 *in* D. N. Hyder, ed., Proc. 1st Internatl. Rangeland Congress.

Harniss, R. O., and K. T. Harper. 1982. Tree dynamics in seral and stable aspen stands of central Utah. USDA For. Serv. Res. Pap. INT-297. 7 pp.

Hilton, J. E., and A. Bailey. 1974. Forage production and utilization in a sprayed aspen forest in Alberta. J. Range Manage. 27(5):375–380.

Hittenrauch, H. R. 1976. Response of aspen to various harvest techniques. *In* Utilization and marketing as tools for aspen management in the Rocky Mountains. USDA For. Serv. Gen. Tech. Rep. RM-29:41–44.

Jones, J. R. 1975. Regeneration on an aspen clearcut in Arizona. USDA For. Serv. Res. Note RM-285. 8 pp.

———. 1976. Aspen harvesting and reproduction. *In* Utilization and marketing as tools of aspen management in the Rocky Mountains. USDA For. Serv. Gen. Tech. Rep. RM-29:30–34.

Jones, J. R., and D. P. Trujillo. 1975. Development of some young aspen stands in Arizona. USDA For. Serv. Res. Pap. RM-151. 11 pp.

Lester, J. E. 1972. The effects of livestock grazing on the response of high mountain vegetation determined from a study of net production and utilization. Unpublished dissertation. Univ. of Wyoming, Laramie. 105 pp.

Little, E. L. 1971. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. USDA For. Serv. Misc. Publ. 1146.

Mueggler, W. F., and D. L. Bartos. 1977. Grindstone Flat and Big Flat exclosures—a 41-year record of changes in clearcut aspen communities. USDA For. Serv. Res. Pap. INT-195. 16 pp.

Mueggler, W. F., and R. B. Campbell, Jr. 1982. Aspen community types on the Caribou and Targhee national forests in southeastern Idaho. USDA For. Serv. Res. Pap. INT-294. 32 pp.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York. 547 pp.

Reed, R. 1971. Aspen forests of the Wind River Mountains, Wyoming. Amer. Midl. Nat. 86:327–343.

Robinson, M. E. 1971. Sheep Creek water evaluation project—a study of vegetative type conversion for water yield improvement. USDA For. Serv., Intermountain Region, Fishlake National Forest, Administrative Study (unpubl.). 280 pp. (64 pp. + 216 pp. appendices).

Sampson, A. W. 1919. Effect of grazing upon aspen reproduction. USDA Bull. 741. 29 pp.

Schier, G. A. 1975. Deterioration of aspen clones in the middle Rocky Mountains. USDA For. Serv. Res. Pap. INT-170. 14 pp.

Smith, A. D., P. A. Lucas, C. E. Baker, and G. W. Scotter. 1972. The effects of deer and livestock on aspen regeneration in Utah. Utah Division of Wildlife Resources, Pub. 72-1. 32 pp.

Youngblood, A. D., and W. F. Mueggler. 1981. Aspen community types on the Bridger-Teton National Forest in western Wyoming. USDA For. Serv. Res. Pap. INT-272. 34 pp.

HIP GLANDS IN A NATURAL POPULATION OF MONTANE VOLES (*MICROTUS MONTANUS*)

Craig R. Groves[1,2] and Barry L. Keller[1]

Abstract.— We recorded the occurrence of hip glands in a population of montane voles (*Microtus montanus*) in southeastern Idaho. Sexual maturity was positively associated with the presence of hip glands in both males and females. Significantly more males than females possessed hip glands. Males and females with hip glands were significantly heavier than individuals without glands. The possible function of hip glands in scent marking, aggression, and population fluctuations is discussed.

Many species of *Microtus* possess hip or flank glands. The histology and taxonomic significance of these sebaceous glands were reviewed by Quay (1968) and Skurat (1969). Howell (1924) first described hip glands in a population of montane voles (*Microtus montanus*) in California. More recently, Jannett (1978) and Lyons (1979) reported the presence of hip glands in populations of *M. montanus* in Wyoming and Idaho, respectively. Although these glands have been examined in several laboratory studies (e.g., Jannett 1981), limited quantitative data are available on the occurrence of these glands in wild populations. During a population study of small mammals in southeastern Idaho, we recorded the presence or absence of hip glands for 86 male and 99 female *M. montanus* (Groves and Keller 1983). The purpose of this paper is to compare reproductive characteristics and weights of voles in which hip glands were present or absent.

Methods

Our research was conducted on the Radioactive Waste Management Complex of the Idaho National Engineering Laboratory Site. Vegetation in the areas where voles were live trapped consisted primarily of crested wheatgrass (*Agropyron cristatum*) that had been seeded over areas where low-level radioactive waste was interred. We recorded data on the occurrence of hip glands during monthly trapping intervals from April to July 1979. Details on the study area and trapping methods are provided in Groves and Keller (1983).

Results and Discussion

Hip glands occurred on 65% of male *M. montanus* (Table 1). There was a positive association between sexual maturity in males and the presence of hip glands ($X^2 = 25.54$, $P < 0.01$). Males with hip glands were significantly heavier than males without glands ($t = 7.75$, $P < 0.01$). Compared to males, fewer females (12%) possessed hip glands ($X^2 = 55.60$, $P < 0.01$). Like males, sexual maturity in females was positively associated with the presence of hip glands ($X^2 = 6.23$, $P < 0.05$). Females with hip glands were also heavier than females without glands ($t = 2.50$, $P < 0.01$).

Howell (1924), Jannett (1978), and Lyons (1979) observed that only a few female *M. montanus* possessed hip glands in wild populations, whereas most well-developed hip glands occurred in large males. Our data support their notions that only a few females possess hip glands in natural populations. In contrast, hip glands occur commonly in both sexes in many species of *Microtus* (Quay 1968).

Our data suggest that weight (age) and sexual maturity are related to the development of hip glands in *M. montanus*. Lyons (1979) reported a positive correlation between mean monthly weights of male *M. montanus* and the percent occurrence of hip glands. Jannett (1978) indicated that hip gland development is androgen-dependent in male and female *M. montanus*, as well as several other microtine species. Clarke and Frearson (1972) positively associated hip gland development in male *M. agrestis* with sexual maturity. Correlations between reproduction and hip gland occurrence were also reported for male and female *M. xanthognathus* (Wolff and Lidicker 1979), male and female *M. townsendii* (MacIsaac 1977), and male *M. californicus* (Lidicker 1980). In a long-term study of population dynamics of *M. pennsylvanicus*, Tamarin (1981) observed only one vole with hip glands, and this individual was an old, sexually mature male. In addition, Boonstra and Youson (1982) reported well-developed hip glands in breeding males of *M. pennsylvanicus* as revealed by histological examination, although no consistent relationship was observed between the degree of hip gland development and breeding status in females.

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Jannett (1981) reported that scent marking with hip glands by male *M. montanus* in the laboratory is rare, although other species of *Microtus* do exhibit marking behavior with hip or flank glands (e.g., Wolff and Johnson 1979). Lyons (1979) conducted laboratory experiments that indicated odors from hip glands of male *M. montanus* may be important for individual and group recognition. Stoddart et al. (1975) compared flank gland secretions for different sexes, age classes, and poulations of *Arvicola terrestris.* They found marked differences between age classes and among populations, suggesting a strong social influence on the quality of flank gland secretions. The precise function of the various specialized glands (Quay 1962, 1965, 1968) in microtine rodents is uncertain, but it would appear that these glands exude chemicals (pheromones) that may facilitate recognition among individuals (Richmond and Stehn 1976, Beard 1978, Lyons 1979, Jannett 1981). Additionally, they may integrate breeding of sexually mature individuals (Keller, in press). Thus, hip gland marking may be important in territorial defense, individual recognition, and other social interactions.

Table 1. Reproductive characteristics and mean weights of montane voles in which hip glands were present or absent. Males with scrotal testes were considered to be in reproductive condition. Females who had previously lactated and/or possessed open pubic symphyses or perforate vaginas were considered to be sexually mature.

	Hip glands	
	Present	Absent
Males		
Number of sexually mature individuals	44	6
Number of individuals not sexually mature	12	24
Mean weight (g) ± S.E. (n)	41.2 ± 1.3 (56)	24.0 ± 2.0 (30)
Females		
Number of sexually mature individuals	12	56
Number of individuals not sexually mature	0	31
Mean weight (g) ± S.E. (n)	39.7 ± 2.1 (12)	29.6 ± 1.5 (87)

Our observations of hip gland occurrence in an increasing *M. montanus* population suggest that these glands may also be important in behavioral changes that occur in fluctuating vole populations (see review, Krebs and Myers 1974). Jannett (1981) has demonstrated that scent secretions from hip glands of male *M. montanus* mediate both intra- and interspecific attacks. He hypothesized that development of hip glands at puberty stimulates aggressive interactions between adult and pubertal voles, and may also reduce recruitment of voles into the breeding population. Future research efforts should investigate the role that secretions from hip glands may play in different phases of a microtine cycle.

Acknowledgments

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Literature Cited

Beard, H. B. 1978. Hormonal influence on the social behavior of the vole, *Microtus ochrogaster*: effects of photoperiod, temperature, gonadectomy, preputialectomy and oral angle gland removal. Unpublished dissertation. Iowa State Univ., Ames. 232 pp.

BOONSTRA, R., AND J. H. YOUSON. 1982. Hip glands in a field population of *Microtus pennsylvanicus*. Canadian J. Zool. 60:2955–2958.

CLARK, J. R., AND S. FREARSON. 1972. Sebaceous glands on the hindquarters of the vole, *Microtus agrestis*. J. Reprod. Fert. 31:477–481.

GROVES, C. R., AND B. L. KELLER. 1983. Ecological characteristics of small mammals on a radioactive waste disposal area. Amer. Midl. Nat. 109:253–265.

HOWELL, A. B. 1924. Individual and age variation in *Microtus montanus yosemite*. J. Agr. Res. 28:977–1015.

JANNETT, F. J., JR. 1978. Dosage response of the vesicular, preputial, anal and hip glands of the male vole, *Microtus montanus*, to testosterone propionate. J. Mammal. 59:772–779.

______. 1981. Scent mediation of intraspecific, interspecific, and intergenic agonistic behavior among sympatric species of voles (Microtinae). Behav. Ecol. Sociobiol. 8:293–296.

KELLER, B. L. In press. Reproductive Variations. *In* Robert H. Tamarin, ed., The biology of *Microtus* (Rodentia). Special Publication 8, American Society of Mammalogists.

KREBS, C. J., AND J. H. MYERS. 1974. Population cycles in small mammals. Adv. Ecol. Res. 8:267–399.

LIDICKER, W. Z., JR. 1980. The social biology of the California vole. Biol. 62:46–55.

LYONS, T. J. 1979. Hip gland occurrence and function in *Microtus montanus*. Unpublished thesis. Idaho State Univ., Pocatello. 50 pp.

MACISAAC, G. L. 1977. Reproductive correlates of hip glands in voles (*Microtus townsendii*). Canadian J. Zool. 55:939–941.

QUAY, W. B. 1951. Apocrine sweat glands in the angulus oris of microtine rodents. J. Mammal. 43:303–310.

______. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angle in rodents. J. Mammal. 46:23–37.

______. 1968, The specialized posterolateral scent gland regions in microtine rodents. J. Mammal. 49:427–445.

RICHMOND, M. E., AND R. STEHN. 1976. Olfaction and reproductive behavior in microtine rodents. Pages 197–216 *in* Mammalian olfaction, reproductive processes and behavior. Academic Press, New York. 344 pp.

SKURAT, L. N. 1969. The structure of sacral glands in some voles (Microtinae). Zool. Zh. 48:1221–1226 (in Russian).

STODDART, D. M., R. T. ALPIN, AND M. J. WOOD. 1975. Evidence for social difference in the flank organ secretion of *Arvicola terrestris* (Rodentia:Microtinae). J. Zool. 177:529–540.

TAMARIN, R. H. 1981. Hip glands in wild-caught *Microtus pennsylvanicus*. J. Mammal. 62:421.

WOLFF, J. O., AND M. F. JOHNSON. 1979. Scent marking in taiga voles. J. Mammal. 60:400–403.

WOLFF, J. O., AND W. Z. LIDICKER, JR. 1980. Population ecology of the taiga vole, *Microtus xanthognathus*, in interior Alaska. Canadian J. Zool. 58:1800–1812.

MULTIPLE USE SYSTEMS FOR AQUACULTURE

J. M. Henderson[1,2], R. A. Heckmann[1] and R. N. Winget[1]

Abstract.— Two recirculating aquaculture systems were constructed using a sequence of five tanks each. Each system contained two plant species, duckweed (*Lemna minor*) and chinese water chestnut (*Eleocharis dulcis*); two fish species, channel catfish (*Ictalurus punctatus*) and tilapia (*Tilapia aurea*); and a freshwater prawn (*Macrobrachium rosenbergii*). Duckweed production during the 132-day experiment reached as high as 87.2 tons/hectare/year (t/ha/yr). Water chestnut production was not successful in the restricted light situation of the lab, but in an outdoor test planting, corn production was 37.2 t/ha/yr. Four feeding trials were attempted using the following percent of fish body weight: 2.5% commercial feed; 5% wet duckweed; 15% wet duckweed; and 15% wet duckweed with 1% commercial feed. Feed to flesh conversion ratios averaged 1.97:1 for the three control tanks and 1.44:1 overall for the treatment tank. The fish-fed duckweed and commercial feed grew as well or better than those fed commercial food alone.

Malnutrition is a serious problem, especially in the developing nations (Mayer 1976). In the United States, annual food production continues to increase despite large losses of prime farmland each year (Jorling 1978). According to Chapman (1969), the biggest problem is not one of food availability, but the lack of protein. Fish and related foods are being developed as alternate protein supplies that can be produced at reasonable prices. There is a great potential for aquaculture in the Great Basin area that includes the multiple use systems, one of which is described in this article.

Approximately 6.4 kg (14 lbs) of fish per capita are consumed annually in the U.S. (USDA 1980). In 1979, over half of this was imported (Holden 1978) at a cost of over $3 billion, according to USDA statistics. Fish is an excellent protein source that is low in fatty acids and under optimal conditions can be produced at costs competitive with other animal products (Ray 1981).

Successful culture of warm water fish requires a constant supply of warm water of approximately 27 C (Caulton 1978, USDA 1973). Most warm water aquaculture in this country is in the south and southeast because of near subtropical weather and abundant surface waters (Flemming 1978, Landreneau 1981, USDA 1973). However, other regions have potential for warm water aquaculture systems if alternate energy sources for heating the water—such as waste heat from coal-fired electrical generation, geothermal water, and solar concentrators—could be used. This could increase the nation's production of fish products and would place the fish closer to the market, thus cutting transportation costs.

The objective of this study was to develop a multiple-use approach to warm water aquaculture involving two species of warm water fish, channel catfish (*Ictalurus punctatus*), and tilapia (*Tilapia aurea*); two species of aquatic plant, duckweed (*Lemna minor*) and chinese water chestnut (*Eleocharis dulcis*); and a freshwater prawn (*Macrobracium rosenbergii*). These species were chosen because of their reported compatibility, high productivity, and marketability (Dunseth 1977, Suffern 1980). The goals for the project were to monitor productivity, water quality, and test feeding of duckweed to catfish and tilapia. A brief description of each of the plant and animal species follows.

Channel catfish was well known as a food fish in the United States. They tolerate a wide range of dissolved oxygen and temperature levels, grow well on artificial feeds, and tolerate crowded conditions associated with intensive culture. Diseases such as *Ichthyophthirius* ("Ich") can cause severe problems if preventative measures are not taken. Due to propagation techniques, large numbers of fingerlings can be produced. Flesh quality and good public image are responsible for their marketability (USDA 1973). Channel catfish are bottom-feeding omnivores that can reach marketable size of 454 g (1 lb) in 8 to 10 months at 27 C (Brown 1977). One farm in Buhl, Idaho, produces up to 4.5 t/ha/yr (2 t/a/yr) at a 2:1 feed conversion ratio (Ray 1981). Other farms have reached feed conversion ratios as low as 1.3 to 1.5:1 (Brown 1977).

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Tilapia are virtually unknown to the United States consumer. In the Far East, Africa, and the Middle East they have been cultured for thousands of years. Tilapia are intolerant to temperatures below 9–15 C (Suffern 1980). They feed low on the food web, eating mostly aquatic macrophytes (Caulton 1978). They also feed on waste products of other aquatic and terrestrial animals (Infanger 1976, Melarney and Todd 1977, Moav et al. 1977, Rumsey et al. 1981). Except for temperature tolerance, tilapia is a hardy species. They have been known to withstand oxygen levels as low as 1 mg/l and salinity as high as 72,000 mg/l (Balarin 1979). At 100 g tilapia become reproductively active with resultant decreased weight gain. To avoid this, hybrid crosses and hormone treatments that result in mostly male offspring have been developed (Shelfon et al. 1978). High-density stocking seems to disrupt social behavior that can slow or stop reproduction (Suffern 1980). Marketable size of 200 to 900 g (0.5 to 2 lbs) can be reached in 12 to 18 months (Lauenstein 1978). Experiments at Oak Ridge, Tennessee, have shown an estimated 56 t/ha/yr can be produced in aerated sewage. Feed conversion for tilapia has been reported at 1.3 to 1.5:1 (Collis and Smitherman 1978, Lauenstein 1978). Test marketing shows this fish has excellent taste and a demand for its meat can be developed (Dunseth 1977).

Duckweed occurs in still or slightly moving waters. Flourishing growth is frequently found in stagnant small ponds or ditches rich in organic matter (Hillman 1961). Duckweed reproduces vegetatively by rapid clonal growth. Under proper conditions, weight can double every 2 to 4 days (Harvey and Fox 1973, Rusoff et al. 1980). Duckweed growth is 2 to 20 times faster than the fastest growing terrestrial plants. Their fronds do not form a complex structure but instead break into colonies. There is a total absence of woody tissue (Hillman and Culley 1978).

Production of duckweed has been reported to reach levels of 20 t/ha/yr (1488 lbs/a/mo) dry weight in some experiments (Said et al. 1979) and as high as 33.6 t/ha/yr (2500 lbs/a/mo) in others (Culley and Epps 1973). In comparison, alfalfa production for 1979 in the United States averaged 7.13 t/ha/yr (3.18 t/a/yr) dry weight (USDA 1980). Crude protein content of alfalfa is around 16% (Hillman and Culley 1978)—duckweed ranges between 20% and 40% (Culley and Epps 1973, Rusoff et al. 1980). In one test duckweed produced more than twice as much protein/ha as the best alfalfa pasture and 10 times as much as soybeans (Walsh and Palmer 1979).

According to Rusoff, Blackeney, and Culley (1980), duckweed protein has potential as a food supplement for animals and they project it could be used as a dietary supplement for man. They found the essential amino acid content of duckweed protein met FAO standards except for methionine. Hillman and Culley (1978) reported that dairy cows will accept up to 75% of the total dry weight of their feed as duckweed with no ill effects.

The chinese water chestnut is a sedge, family Cyperaceae. It grows to a height of five feet and reproduces through rhizomes and corms. Corms are widely used in Chinese cooking. Corms 25–30 mm in diameter are most useful for sale while smaller, and larger corms are used for propagation or animal feed (Squires 1979). Tops can be used as an animal's food supplement. In ponds at Clemson University, chinese water chestnut corms are produced at a rate of 4,664 kg/ha/yr (2.08 t/a/yr) (McCord and Loyacano 1978). These ponds had lower levels of NO_3 and NH_4-Nitrogen than those without water chestnuts. Effectiveness of nutrient removal by aquatic plants is affirmed by Boyd (1970).

Disadvantages to water chestnut and duckweed production are cost of harvest and removal of water from plant tissue. Duckweed contains as much as 95% water (Rusoff et al.

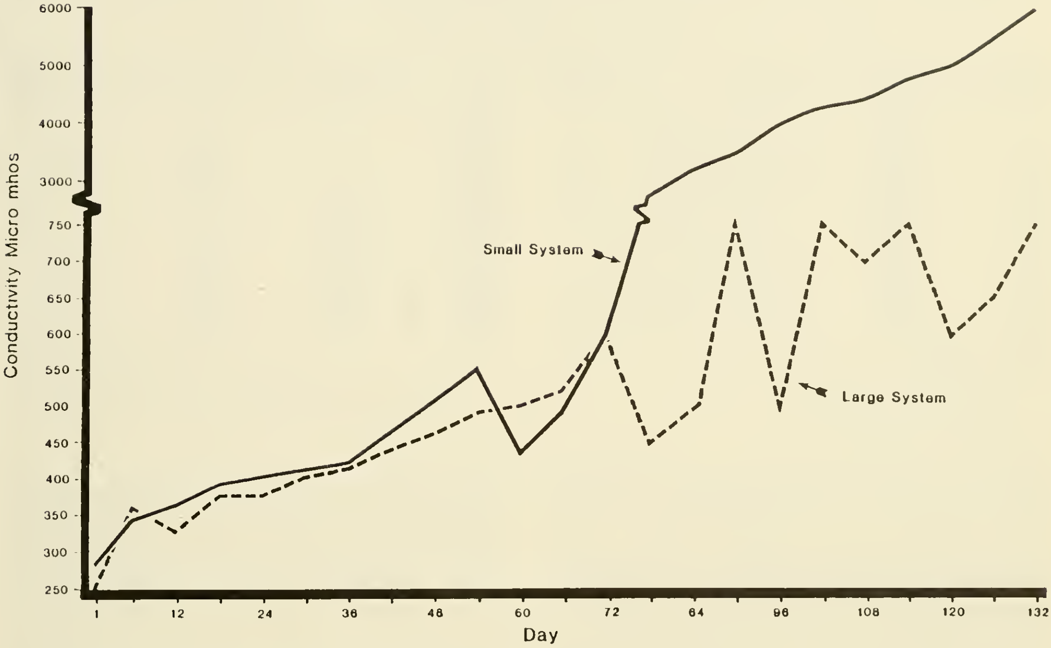


Fig. 1. System design, capacity, and directions of water flow.

1980). Koegel, Livermore, and Bruhn (1975) found that harvesting rooted aquatic plants costs $60–$94 per acre, which is higher than expected for duckweed, which could be skimmed off the surface (Culley and Epps 1973). Plants can be dried by various methods, including sun drying and oven drying (Lawson et al. 1974).

Macrobrachium rosenbergii is the most popular freshwater prawn under cultivation in the United States. It must be maintained in warm water because its intolerance to cold temperatures is similar to that of tilapia (Stickney 1979). Shang and Fujimura (1977) studied the economics of establishing a *M. rosenbergii* operation in Hawaii, evaluating ponds ranging in size from 0.4 to 40 hectares. These authors determined that at a price of $6.60/kg (based on reasonable wholesale prices in Hawaii), a farm for freshwater prawns would become profitable if it were at least 4 hectares in area. *Macrobrachium* species require water of low salinity during spawning and larval development but may spend the remainder of their lives in fresh water (Bardach et al. 1975).

MATERIALS AND METHODS

Two recirculating systems, with no outflow, involving a sequence of five tanks each were constructed (Fig. 1). The large system had approximately twice the capacity of the small system. The experiment covered 132 days. Two tanks per system contained tilapia and channel catfish. Another two tanks per system contained duckweed. Into one duckweed tank per system were placed 25 freshwater prawn, each 1 cm long. Into the other two duckweed tanks were placed two tilapia each (6.3 g combined weight in the large system, 9.3 g in the small system). The fifth tank in each system contained the biological filter composed of crushed oyster shell and *Nitrosomonas* and *Nitrobacter* nitrifying bacteria (Stickney 1979). The filter tanks contained 10 six-inch clay pots in the large system and 5 in the small system, with three water chestnut corms planted in each pot.

The water in each system was circulated from the filter tank into the first duckweed tank, then into the first fish tank, next into a second duckweed tank, then a second fish

TABLE 1. Large system lower tank (weights, feed, conversions). Day 1 = 25 February 1981.

	Fish weights (g)							
	Catfish		Tilapia			Feed (g)		Conversion
Day	Wt.	% gain	Wt.	% gain	Total	Duckweed	Commercial	(feed/flesh)
1	58.4		182.6		241.0			
14	104.3	79	265.8	46	370.1		78.0	0.60
30	145.0	39	400.8	51	545.8		148.8	0.85
45	213.2	47	619.2	54	832.4		257.1	0.90
60	186.7	0	590.4	0	777.1	691.5	0	0
75	178.8	0	608.5	3	787.3	1631.0*	0	0
91	124.0	0	695.5	14	819.5	1576.0*	105.4	8.17
100	155.9	26	761.5	9	917.4	1106.1*	73.8	1.88
117	230.5	48	930.0	22	1160.5	2201.6*	147.2	1.51
132	293.5	27	1202.0	30	1495.5	54.0*	273.2	0.83

Total gain = 1254.5 g
Total feed—duckweed = 726.0 g dry wt
—commercial = 1083.5 g
Overall conversion = 1.44
*Duckweed from an outside source

tank, and back into the filter (Fig. 1). Well water was used in the large system for the entire experiment but in the small system only for the first 77 days. On day 77 well water was changed over to waste water effluent from a coal-fired power generation plant.

Catfish and tilapia received a pelleted commercial catfish food fed at 2.5% of their body weight per day. The rate was adjusted on 15-day intervals according to the growth of the fish. In the large system, beginning on day 45 of the experiment, duckweed was substituted for the commercial food in one fish tank. Duckweed was fed to the fish at the rate of 5% of the fish's weight per day for two weeks, then 15% for the next two weeks, and finally 15% duckweed supplemented by 1% dry weight commercial food for the remainder of the experiment. Fish and prawns in the duckweed tanks fed on existing plants and waste materials that flowed through the system. Duckweed was harvested as necessary to promote maximum growth and prevent clogging of screens. The wet weight of duckweed harvested was recorded. Standard florescent lamps provided light for all plant growth except for wide spectrum florescent lamps over the water chestnuts in the large system. The lamps were set on 16-hour on and 8-hour off time periods.

Oxygen, temperature, pH, conductivity, and nitrite levels were measured daily. Temperature and conductivity were measured with a standard conductivity meter. Oxygen and pH were measured with an Altex Selec-Ion 5000 ion analyzer with Orion Research

TABLE 2. Large system upper tank (weights, feed, conversions) Day 1 = 25 February 1981.

	Fish weights (g)						
	Catfish		Tilapia				Conversion
Day	Wt.	% gain	Wt.	% gain	Total	Feed (g)	(feed/flesh)
1	48.3		193.9		242.2		
14	75.2	56	272.6	41	347.8	79.3	.75
30	119.4	59	377.5	39	496.9	139.2	.93
45	157.8	32	541.9	44	699.7	223.2	1.10
60	200.7	27	725.0	34	925.7	262.5	1.16
75	261.0	31	937.0	29	1198.0	324.8	1.19
91	280.8	8	976.7	4	1257.5	420.0	7.06
100	319.2	14	1063.4	9	1382.6	282.6	2.26
117	347.2	9	1127.5	6	1474.7	553.6	6.01
132	431.0	24	1308.0	16	1739.0	479.7	1.81

Total gain = 1496.8 g
Total feed = 2764.9 g (commercial)
Overall conversion = 1.85

TABLE 3. Small system upper tank (weights, feed, conversions) Day 1 = 25 February 1981.

	Fish weights (g)						
	Catfish		Tilapia				
Day	Wt.	% gain	Wt.	% gain	Total	Feed (g)	Conversion (feed/flesh)
1	28.2		123.4		151.6		
14	42.6	50	183.8	49	226.4	49.4	0.66
30	45.0	7	251.7	37	296.7	91.2	1.30
45	62.7	38	354.1	41	416.8	133.2	1.11
60	93.5	50	446.8	26	540.3	156.0	1.26
75	10.5	0	237.0	0	247.5	165.5	0°
91	16.5	60	333.7	41	350.2	93.0	0.91
100	20.0	25	348.1	5	368.1	79.2	4.42
117	39.0	95	459.0	32	498.0	147.2	1.13
132	42.0	10	546.0	23	606.0	162.5	1.50

Total gain = 454.4 g
Total feed = 1077.2 g (commercial)
Overall conversion = 2.37 (due to high mortality from day 60–75)
°Mortality due to low D.O. and feeding stress

probes. Nitrite light transmittance levels were measured with a Bausch and Lomb Spectronic 20 using sulfanilamide and dihydrochloride solutions and standard test procedures (Spotte 1970).

RESULTS

For the first 45 days of the experiment, fish in all tanks were fed commercial feed. The fingerling catfish showed gains of up to 79% of body weight each 15-day period during the first 45 days. The tilapia showed similar gains during the same initial period. As a result, the feed to flesh conversion ratio for both ranged from 0.60:1 to 1.30:1 (Tables 1 to 4). The rapid growth spurt is expected from fingerlings. All fish showed general declines in percent growth every 15 days through the rest of the experiment (increased conversion ratio). Major declines in growth rates in the control tanks after day 45 were the result of mortality from low dissolved oxygen levels. In the treatment tank, the fish fed only duckweed at the 5% level lost weight (Table 1) between days 45 to 60. When fed duckweed at 15% from day 60 to 75, the catfish continued to lose weight but tilapia increased in weight slightly. The 15% level of duckweed was supplemented with 1% commercial food from day 76 through the rest of the experiment. Under this regime the tilapia began to increase in weight more rapidly, but the catfish, due to mortality of some of the fish, lost weight between days 75 and 91, probably due to overnight low oxygen stress. Both tilapia and catfish in the treatment tank from day 91 responded to the

TABLE 4. Small system lower tank (weights, feed, conversions) Day 1 = 25 February 1981.

	Fish weights (g)						
	Catfish		Tilapia				
Day	Wt.	% gain	Wt.	% gain	Total	Feed (g)	Conversion (feed/flesh)
1	28.5		96.0		124.5		
14	30.0	7	140.5	46	170.5	40.3	0.88
30	43.1	43	180.0	29	223.1	60.8	1.16
45	61.0	42	275.5	53	336.5	100.8	0.89
60	94.0	54	378.5	36	472.5	126.0	0.93
75	118.0	26	474.5	26	592.5	165.2	1.38
91	94.3	0	506.2	7	600.5	217.0	0°
100	119.7	27	536.5	6	656.2	135.0	2.42
117	170.5	43	603.0	13	773.5	262.4	2.24
132	203.0	19	717.0	20	920.0	250.9	1.71

Total gain = 795.5 g
Total feed = 1358.4 g (commercial)
Overall conversion = 1.71
°Mortality due to low D.O. from day 75–91.

combined diet and equaled or exceeded the weight gains in the three control tanks. The overall conversion ratios for the four fish tanks were 1.44:1 in the treatment tank and 1.71 to 2.37:1 in the three control tanks.

The two tilapia in the lower duckweed tank of the large system grew from 6.2 g to 77.0 g in 75 days. This was more gain per day than the fish in any of the fish tanks. Though not fed, they were free to feed upon existing plants and waste entering their tank. No duckweed was harvested from this tank because the fish kept its biomass low. The fish placed into the small system's lower duckweed tank had similar growth, increasing from 9.3 g to 42 g in 34 days. Their presence was a factor in that tank's lower duckweed production during days 1 through 45 (Table 5).

TABLE 5. Duckweed production (Day 1 = 25 Feb. 1981).

	Amount harvested (g)		
Date	Large system upper tank	Small system upper tank	Small system lower tank°
2 April	458.2	317.1	250.8
20	698.9	–	–
22	–	266.0	139.7
12 May	275.0	319.5	–
20	126.0	–	–
21	–	–	203.0
23	–	170.0	–
27	327.0	–	–
30	–	192.0	–
2 June	–	142.0	–
4	286.0	–	–
8	129.0	–	–
13	–	140.0	–
14	–	–	138.0
15	135.0	–	–
16	135.0	–	–
17	135.0	–	–
19	135.0	–	–
20	135.0	–	–
21	–	70.0	70.0
23	44.0	–	–
24	–	–	54.0
25	102.0	–	–
26	45.0	–	–
27	57.0	–	–
29	45.0	–	–
30	110.0	–	–
1 July	63.0	–	–
2	40.0	–	–
6	65.0	–	–
Totals (g)	3546.1	1616.6	975.7
t/ha/hr	82.3	87.2	52.4
(t/a/yr)	36.7	38.9	23.4

°Fish were included in this tank.

Due to small size (1 cm) the 25 freshwater prawns placed in each system were not weighed or measured until day 75. The prawns were left to feed on plants, algae, and waste products of the system. By day 75, they averaged 3 cm in length, but numbers had dropped from 25 per tank to approximately 15, probably due to oxygen-stress-induced mortality and cannibalism. By day 132, 10 remained per tank with an average length of approximately 5 cm.

On day 1 the duckweed tanks were each innoculated with 10 g of duckweed in the small system and 20 g each in the large system. The presence of fish precluded duckweed harvest from the large system's lower tank. Duckweed production was between 52.4 and 87.2 t/ha/yr (23.4 to 38.9 t/a/yr) for the three remaining tanks containing duckweed (Table 5). The lower figure (52.4 t/ha/yr) was a result of tilapia foraging in the small system's lower tank. Low dissolved oxygen levels were attributed to high respiration rates of plants and biological filter organisms (Fig. 2).

Chinese water chestnuts did not grow well in the lab because of light limitations. Standard florescent lamps over the large filter were replaced with wide spectrum florescent lamps at day 75, but there was only a slight improvement in growth noticed. Plants continued to live but reached a maximum height of only 0.6 m, and no corms were produced by these plants. At the Hegerhorst system in Benjamin, Utah, water chestnuts from the same stock planted in an outdoor pond reached a height of over 1.5 m. Production was 237 t/ha/yr (106 t/a/yr) total biomass and 37.2 t/ha/yr (16.6 t/a/yr) corm production.

With the exception of oxygen and nitrite, water quality parameters remained within acceptable limits for the test plants and animals. At times, oxygen concentrations dropped and stressed the catfish, tilapia, and prawns (Fig. 2). Figure 3 shows that between days 9 and 35 the nitrite (NO_2) levels were high in both systems. Nitrifying bacteria had not become established in sufficient numbers to handle the heavy organic load from fish feed and wastes. As bacteria numbers increased, the nitrite levels dropped into acceptable ranges in both systems. The pH

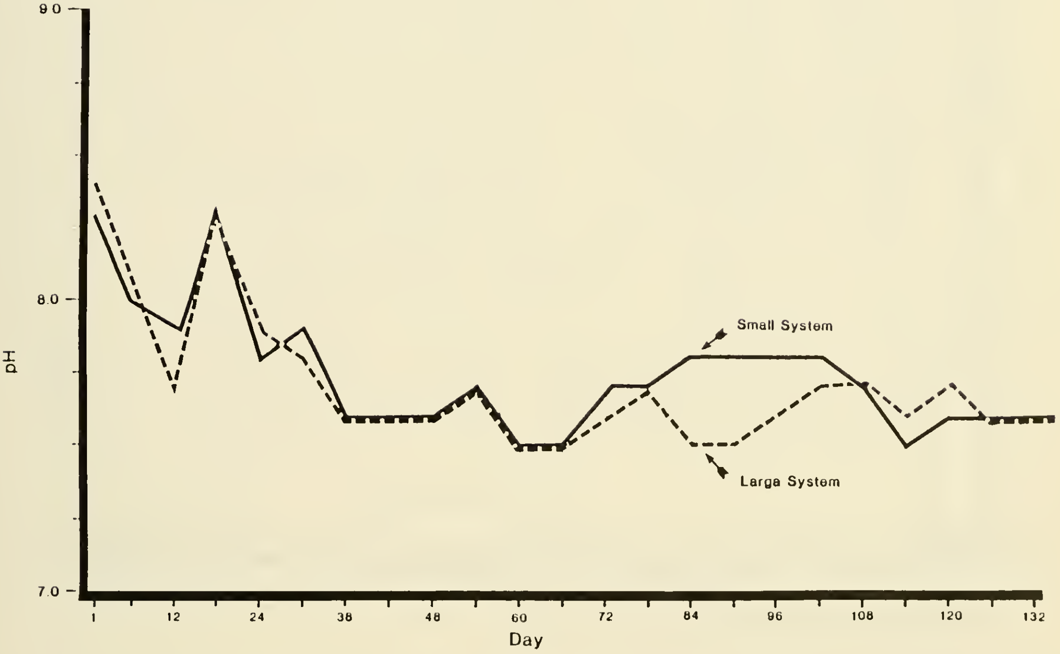


Fig. 2. Oxygen concentration in large and small systems expressed as milligrams per liter (ppm) during 132-day research period (data points every 6th day).

remained fairly constant between 7.5 and 8.0 through the entire experiment (Fig. 4). Conductivity started low but steadily increased because of evaporation through the 132nd day (Fig. 5). Means and ranges of water quality parameters are shown in Table 6.

The increase in conductivity on day 77 in the small system was due to the change from well water to evaporation pond water from a coal-fired generation station. There were no significant variations in production that could be attributed to the new water. Tilapia spawned during this time in the lower tank. The fry were placed in the lower duckweed tank of the large system and after 79 days averaged 5.3 g and 60.5 mm each, feeding only upon plants, algae, and waste products.

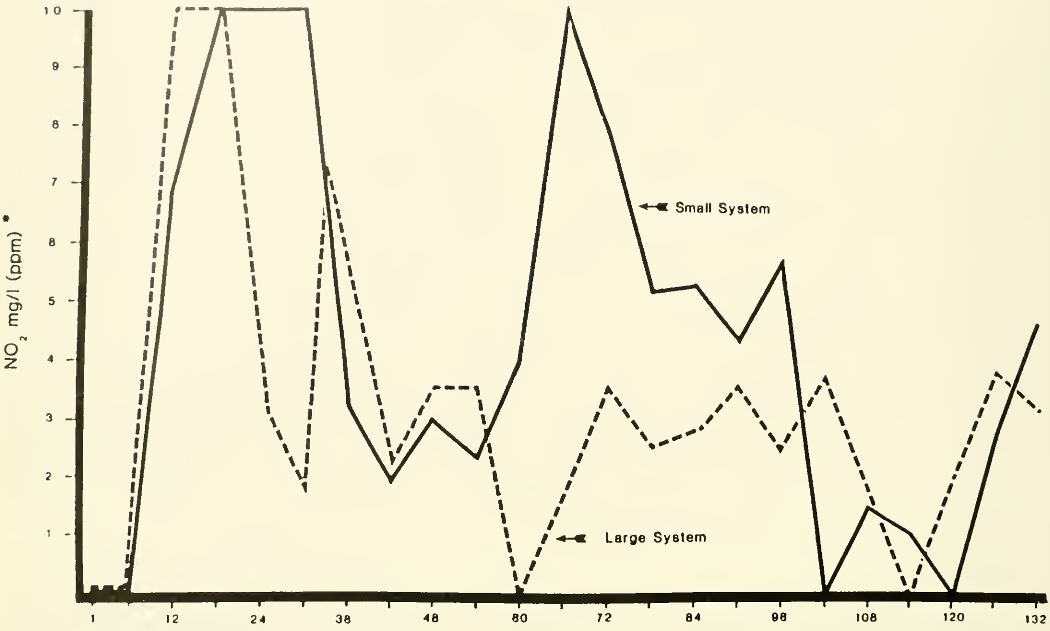
DISCUSSION

Catfish, though observed to occasionally feed on duckweed, are bottom feeders and did not adjust to feeding on floating duckweed. Catfish readily consumed tilapia fecal

TABLE 6. Water quality summary.

	Large system		Small system	
Parameter	Mean	Range	Mean	Range
Temperature (C)	26.8	23.0–31.0	27.2	25.0–30.0
pH	7.7	7.4–8.5	7.7	7.2–8.4
Conductivity (umho's)	535	250–800	510/4930°	440–600/2900/6000°
Oxygen (mg/l)	3.95	1.62–7.2	5.14	1.26–7.80

°Higher conductivity levels are the result of the change from well water to evaporation pond water.



1.0 on this scale equals 1.0 ppm or greater
Any measurement less than 0.1 ppm NO_2 was recorded as 0

Fig. 3. Nitrite concentration in large and small systems expressed as milligrams per liter (ppm) during 132-day research period (data points every 6th day).

strands, which were green in color from consumed duckweed. Growth of catfish indicates an available food value in tilapia wastes. Prawns grew quite readily in the system feeding only on in-system plants plus wastes from the fish. Low dissolved oxygen levels and cannibalism reduced their numbers, indicating a need for aeration and cover if prawns are to be a productive component of this system.

Tilapia will accept duckweed as food. When duckweed was first offered, neither catfish nor tilapia readily fed on the plant. After a few days tilapia readily consumed the duckweed. The delay in accepting duckweed may have been the result of preconditioning to commercial food. Best growth occurred when duckweed was supplemented with commercial feed, suggesting that duckweed may be lacking (Rusoff et al. 1980) in some nutrients needed for proper fish growth. Further research is needed on feeding plants to tilapia.

Duckweed grew well under the standard florescent lights. It supplied a source of food and also improved water quality by removing nitrogen and adding oxygen during the light phase. Plant respiration during the dark phase did decrease oxygen levels and stress the animals. For this reason air was added via an air stone in each tank. Duckweed production may be enhanced with sunlight. Chinese water chestnuts did not grow well in the laboratory under artificial lights, but the chestnuts grown outside at the Hegerhorst farms reached maturity and produced corms, suggesting that light was a limiting factor in the lab. In future experiments this must be taken into consideration.

The main problems encountered with water quality were low oxygen levels and high nitrite levels. Oxygen, through aeration, was added to counteract biochemical oxygen demand (BOD) and plant respiration. It was also needed by the filter organisms for conversion of ammonia to nitrate. During the

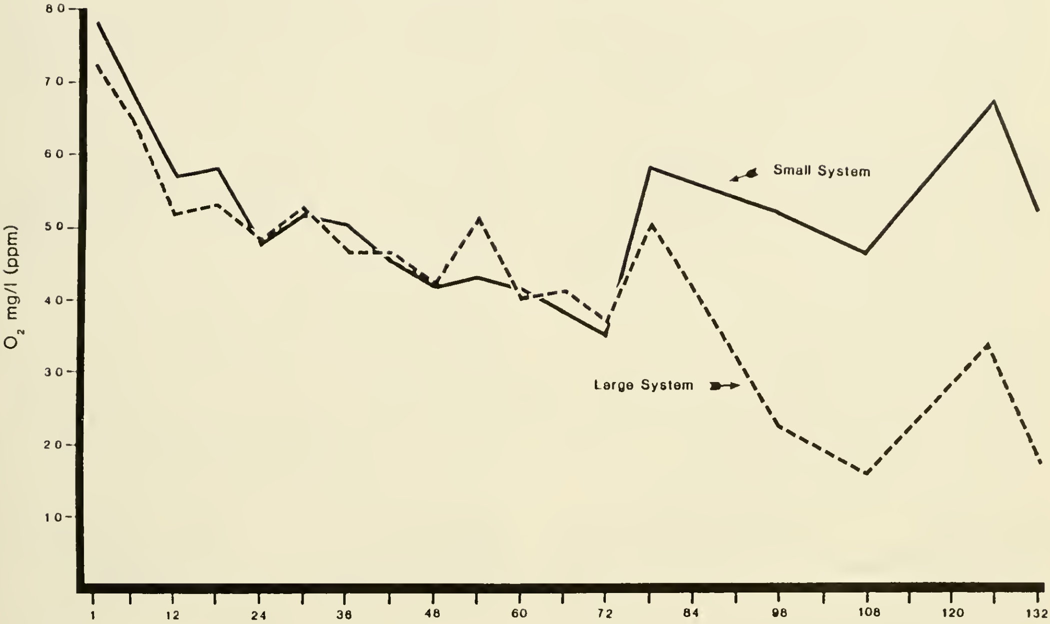


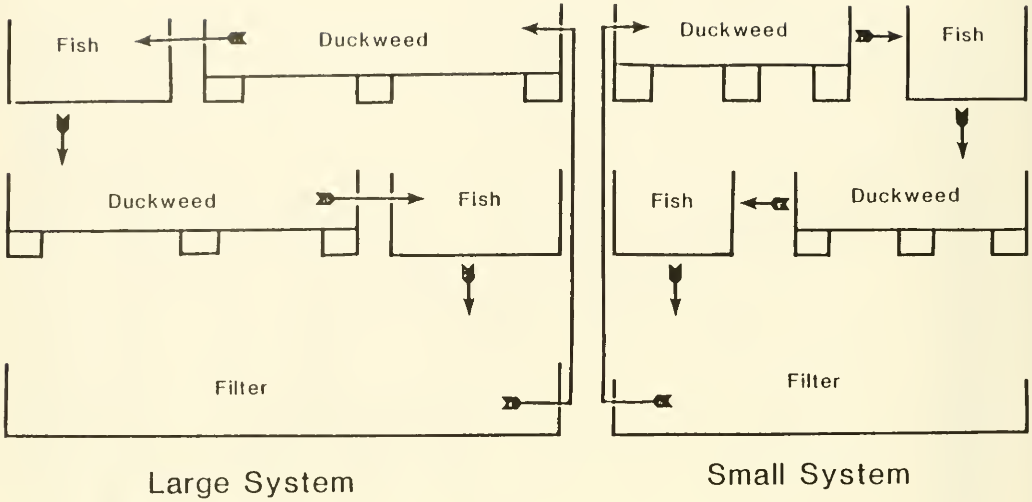
Fig. 4. Water pH in large and small systems during 132-day research period (data points every 6th day).

early stages of the experiment, the nitrogen loading from fish food and wastes caused nitrite levels to exceed 1 mg_ (1 ppm), stressing both tilapia and catfish as evidenced by their "gulping" action at the water surface. After filter organisms became established and oxygen was added, high nitrite levels were no longer a problem.

The closed, recirculating, polyculture system is economically feasible and energy efficient, especially when duckweed, produced using waste nutrients from within the system, is reintroduced as a supplemental food. The USDA Economic and Statistical Service (USDA 1981) reports that feed and fingerlings account for 75% to 80% of production costs in most aquaculture projects. A typical catfish feed contains soybean, corn, and fish meal protein. The costs for these ingredients continue to escalate. Duckweed as a food supplement can help cut project feed costs by maintaining a low commercial feed to fish tissue conversion ratio. Duckweed could be grown in shallow ponds less than 0.5 m deep enriched by waste from livestock or fish systems.

The five plant and animal species used in this study would provide useful and marketable products. Tilapia and catfish have been sold for $1.20 to $2.40/lb dressed weight depending on the geographical area. Freshwater prawns have retailed for as much as $5.00 to $7.00/lb and water chestnut corms for around $1.00 to $2.00/lb. The economic values of this type of polyculture system are obvious—the more that is produced per unit of nutrient and energy input, the better the cost to benefit ratio. Although this system will produce a protein source suitable for human consumption, it can also produce other benefits.

1. The system could provide a secondary use of industrial waste heat and water.
2. Waste heat and water from geothermal projects could be used in this type of system.
3. Alcohol production is a potential use for duckweed or other aquatic plants produced in aquaculture operations. Waste heat, water, and nutrients from alcohol production might also be used in a polyculture system.



Filter tank I.D.	0.69 × 2.39 × 0.31 m	Filter tank I.D.	0.42 × 1.80 × 0.23 m
Fish tanks I.D.	0.64 × 0.69 × 0.38 m	Fish tanks I.D.	0.43 × 0.51 × 0.38 m
Duckweed tank I.D.	0.69 × 1.50 × 0.23 m	Duckweed tank I.D.	0.43 × 1.04 × 0.23 m
Total system capacity	923.6 liters	Total system capacity	546.5 liters
Total surface area, duckweed tank	2.53 m^2	Total surface area, duckweed tank	0.89 m^2

Larger system is 2.4 times larger than the small system

Fig. 5. Water conductivity in large and small systems during 132-day research period (data points every 6th day).

4. Surface farming operations could use nutrient-enriched water flowing from aquaculture operations.
5. The aquaculture operations are nonconsumptive of water. Loss of water is mostly limited to evaporation.
6. Duckweed could be used as a protein supplement for cattle. Other aquatic plants could prove equal or better for this purpose than duckweed.

This study was conducted in a laboratory situation, and results may not necessarily reflect what would happen on a larger scale. Energy budgets were not addressed in this study and are subjects for future experimentation. The actual value of these benefits are subjects for future research under pilot plant or production conditions. Future designs might include rotating, contact, or trickling filters directly in or over the top of individual raceways. The use of alternate energy sources to heat the water is growing in interest. Solar domes, collectors, and concentrators appear potentially valuable as sources of energy for aquaculture systems, especially in areas where water is available but temperatures are not suitable for warm water aquaculture. Aquaculture can provide a high-protein, low-fat product to consumers and at the same time provide diversity and stability to agriculture and agribusiness in many areas of the nation. Aquaculture can provide landowners a use for resources considered marginal for other uses. It can provide an alternative or complementary source of income.

ACKNOWLEDGMENTS

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LITERATURE CITED

BALARIN, J. D. 1979. Tilapia—A guide to their biology and culture in Africa. University Press, Univ. of Stirling. Stirling, Scotland. 174 pp.

BARDACH, J. E., J. H. RYTHER, AND W. O. MCLARNEY. 1972. Aquaculture. Wiley Interscience, New York. 868 pp.

Brown, E. E. 1977. World fish farming: Cultivation and economics. Avi Publishing Company, Inc. Westport, Conn. 397 pp.

Boyd, C. E. 1970. Vascular plants for mineral nutrient removal from polluted waters. Economic Botany 24:95–103.

Caulton, M. S. 1978. The importance of habitat temperatures for growth in the tropical cichlid *Tilapia rendalli* Boulenger. J. Fish Biology 13:99–112.

Chapman, W. M. 1969. Fishing in the future. Ceres FAO Review 2:22.

Collis, W. J., and R. O. Smitherman. 1978. Production of *Tilapia* hybrids with cattle manure or a commercial diet. Pages 43–54 *in* R. O. Smitherman, W. L. Shelton, J. H. Grover, eds. Culture of Exotic Fishes Symposium proceedings. Fish Culture Section, American Fisheries Society, Auburn, Alabama.

Culley, D. D., and E. A. Epps. 1973. Use of duckweed for waste treatment and animal feed. J. Water Pollution Control Federation 45:337–347.

Dunseth, D. R. 1977. Polyculture of channel catfish (*Ictalurus punctatus*), silver carp (*Hypophthalmichthys molitrix*), and three all male tilapias (*Sarotherodon* spp.). Unpublished dissertation. Auburn Univ.. 62 pp.

Flemming, R. C. 1978. Wealth of water. Soil Conservation 43:20.

Harvey, R. M., and I. L. Fox. 1973. Nutrient removal using *Lemna minor.* J. Water Pollution Control Federation 45:1928–1938.

Hillman, W. S. 1961. The Lemnaceae, or duckweeds: a review of the descriptive and experimental literature. Botanical Review 27:221–287.

Hillman, W. S., and D. D. Culley, Jr. 1978. The uses of duckweed. American Scientist 66:442–451.

Holden, C. 1978. Government seeking ways to encourage aquaculture. Science 200:33–35.

Infanger, R. C. 1976. Potential diets for carp production. Unpublished thesis. Brigham Young Univ. 72 pp.

Jorling, T. 1978. Protecting land resources for food and living. J. Soil and Water Conservation 18:213–214.

Koegel, R. G., D. F. Livermore, and H. D. Bruhn. 1975. Harvesting aquatic plants. Agricultural Engineering 56:20–21.

Landreneau, B. C. 1981. Crawfish culture in Louisiana. Paper given at the Annual Meetings of the Soil Conservation Society of America. Spokane, Washington.

Lauenstein, P. C. 1978. Intensive culture of *Tilapia* with geothermally heated water. Pages 82–85 *in* R. O. Smitherman, W. L. Shelton, J. H. Grover, eds., Culture of Exotic Fishes symposium proceedings. Fish Culture Section, American Fisheries Society, Auburn, Alabama.

Lawson, T. B., H. J. Braud, and F. T. Wratten. 1974. Methods of drying duckweed, Lemnaceae. American Society of Agricultural Engineers, Paper no. 74-3531.

McCord, C. L., Jr., and H. A. Loyacano, Jr. 1978. Removal and utilization of nutrients by chinese water chestnut in catfish ponds. Aquaculture 13:143–155.

Mclarney, B., and J. Todd. 1977. Aquaculture on a reduced scale. Commercial Fish Farmer 3:10–17.

Mayer, J. 1976. The dimensions of human hunger. Scientific American 235:40–49.

Moav, R., G. Wohlfarth, G. L. Schroeder, G. Hulata, and H. Baraish. 1977. Intensive polyculture of fish in freshwater ponds. 1: Substitution of expensive feeds by liquid cow manure. Aquaculture 10:25–43.

Ray, L. 1981. Channel catfish and tilapia production in geothermal water. Paper given at the Annual Meetings of the Soil Conservation Society of America. Spokane, Washington. August 2–5.

Rumsey, G. L., M. Cacace, R. R. Zall, and D. J. Lisak. 1981. Dairy processing wastes as a replacement protein source in diets of rainbow trout. Prog. Fish Culturist 43:86–88.

Rusoff, L. L., E. W. Blackeney, Jr., and D. D. Culley, Jr. 1980. Duckweeds (Lemnaceae family) a potential source of protein and amino acids. J. Agriculture Food Chemistry 28:848–850.

Shang, Y. C., and T. Fujimura. 1977. The production economics of fresh water prawn (*Macrobrachium rosenbergii*) farming in Hawaii. Aquaculture 11:99–110.

Said, Z. M., D. D. Culley, L. L. Standifer, E. A. Epps, R. W. Myers, and S. A. Boney. 1979. Effect of harvest rate, waste loading, and stocking density on the yield of duckweeds. Paper presented at the 10th Annual Meeting of the World Mariculture Society, Honolulu, Hawaii.

Shelton, W. L., K. D. Hopkins, and G. L. Jensen. 1978. Use of hormones to produce monosex *Tilapia* for aquaculture. Pages 10–33 *in* R. O. Smitherman, W. L. Shelton, J. H. Grover, eds. Culture of Exotic Fishes symposium proceedings. Fish Culture Section, American Fisheries Society, Auburn, Alabama.

Spotte, S. 1970. Fish and invertebrate culture: water management in closed systems. John Wiley and Sons, New York. 145 pp.

Squires, L. E. 1979. A review of algal and vascular aquatic plant applications in aquaculture. Report prepared for the Aquatic Ecology Laboratory, Brigham Young University, Provo, Utah. 102 pp.

Stickney, R. R. 1979. Principles of warm water aquaculture. John Wiley and Sons, New York. 375 pp.

Suffern, J. S. 1980. The potential of tilapia in U.S. aquaculture. Aquaculture 6:14–18.

U.S. Department of Agriculture. 1980. Agriculture statistics for 1980. United States Government Printing Office, Washington, D.C.

U.S. Department of Agriculture, Economics and Statistical Service. 1981. Aquaculture outlook and situation report. U.S. Government Printing Office, Washington, D.C.

U.S. Department of Interior. 1973. Second report to the fish farmers. Resource Publication 113. Bureau of Sport Fisheries and Wildlife. U.S. Government Printing Office, Washington, D.C.

Walsh, M. A., and J. M. Palmer. 1979. Duckweed—not just for the birds. Utah Science 40:82–85.

ADDITIONS TO THE VASCULAR FLORA OF WYOMING

Erwin F. Evert[1] and Ronald L. Hartman[2]

Abstract.— Eight species previously unreported for Wyoming are listed. A range extension is noted for *Erigeron humilis*, and *Cymopterus bipinnatus* is verified as occurring in Wyoming.

Recent field work has resulted in the addition of eight taxa to the vascular flora of Wyoming. The arctic-alpine species *Erigeron humilis* Grah. is reported for the first time outside the Bighorn Mountains in Wyoming. In addition, Dorn's report (1977) of the occurrence of *Cymopterus bipinnatus* Wats. in Wyoming is confirmed.

Apiaceae

Cymopterus bipinnatus **Wats.** Wyoming, Lincoln Co., 6.4 km W of Kemmerer (T21N R116W S7), 2148 m, 10 Jun 1946, *H. Ripley* & *R. Barneby 7874*, NY; ca 16 km N of Kemmerer, 2194 m, 9 May 1973, S. *Waite* & *K. Harper s.n.*, UC; 19.2 km SW of Diamondville (T19N R118W S1), 2133 m, 6 Jul 1983, *R. Hartman 15739*, RM. Park Co., ca 1.6 km S of Trough Spring, NW side of Rattlesnake Mountain (T54N R104W S35 SW¼), 2590 m, 27 Jun 1980, *E. Evert 1912*, MOR, RM; 64 km E of Cody (T52N R107W S22,28), ca 2042 m, 22 Jun 1983, *M. Lavin 4428*, RM, UC. Fremont Co., ca 12.8 km NE of Dubois (T42N R106W S12 NE¼), 2500 m, 8 Jun 1981, *D. Rizor* & *D. Jones 77*, RM. These records confirm Dorn's report (1977) of the occurrence of this species in Wyoming.

Asteraceae

Centaurea cyanus **L.** Wyoming, Park Co., along Rt. 14 ca 1.3 km W of Wapiti (T52N R105W S23 SW¼), 1735 m, 19 Sept 1982, *E. Evert 5079*, RM. First report for Wyoming.

Erigeron humilis **Grah.** Wyoming, Park Co., Absaroka Range, at the head of Canyon Creek, ca 10 km S of Rt. 14 (T51N R106W S24 NE¼), 3172 m, 14 Jul 1981, *E. Evert 3173*, RM; E side of Buttress Mountain, ca 8 km N of Rt. 14 (T53N R108W S35 SW¼), 3142 m, 28 Jul 1981, *E. Evert 3313*, RM; SW side of Whirlwind Peak, ca 11 km N of Rt. 14 (T53N R108W S16 SE¼), 3172 m, 6 Aug 1981, *E. Evert 3428*, MOR, RM. This arctic-alpine species was previously known in Wyoming from two collections in the Bighorn Range (Lofgren 1956). The collections from the Absaroka Range reported here are 225 km west of the Bighorn Range.

Boraginaceae

Cryptantha spicilifera **(Piper) Payson.** Wyoming, Park Co., W ridge leading to the summit of Heart Mountain (T54N R102W S8), 1891 m, 1 Jul 1981, *R. Hartman 13378*, RM. Park Co., summit of Cedar Mountain, ca 8 km W of Cody (T52N R102W S8 NW¼), 2379 m, 7 Jul 1981, *E. Evert 3013*, RM. First reports for Wyoming.

Campanulaceae

Campanula rapunculoides **L.** Wyoming, Park Co., along Rt. 14 ca 0.4 km E of Gunbarrel Creek (T52N R107W S30 SW¼), 1951 m, 15 Sept 1982, *E. Evert 5015*, RM. First report for Wyoming.

Equisetaceae

Equisetum sylvaticum **L.** Wyoming, Sheridan Co., Bighorn Range, along Sawmill Pass–Red Grade Rd. ca 0.2 km W of Preacher Rock (T54N R86W S31 NW¼), 2501 m,

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26 Jul 1982, *E. Evert 4470*, MOR, RM. Crook Co. (T51N R60W S33 NE¼), 1800 m, 27 Jul 1982, *R. Dorn 3777*, RM. First reports for Wyoming.

LAMIACEAE

Mentha spicata **L.** Wyoming, Park Co., 0.4 km N of Rt. 14 along Aspen Creek (T52N R107W S23 NE¼), 1981 m, 15 Sept 1981, *E. Evert 3356*, RM. First report for Wyoming.

MORACEAE

Morus alba **L.** Wyoming, Park Co., Shoshone Canyon, ca 100 m E of Buffalo Bill Dam (T52N R103W S1 SE¼), 1586 m, 29 May 1980, *R. Hartman 11299*, RM. Same location, 1 Jul 1982, *E. Evert 4087*, MOR, RM. First reports for Wyoming.

POACEAE

Hordeum distichon **L.** Wyoming, Sheridan Co., Whitney Coal Site (T58N R83W S31), 1081 m, 15 Jul 1977, *Brink 1414*, RM. Sweetwater Co., ca 32 km NW of Green River (T20N R109W S16), 1891 m, 11 Jul 1978, *R. Smith 15*, RM. Park Co., along Rt. 14 ca 0.4 km W of Buffalo Bill Dam (T52N R103W S12 NE¼), 1647 m, 6 Aug 1982, *E. Evert 4680*, RM. Park Co., along Rt. 14 ca 0.4 km E of Goff Creek (T52N R108W S23 NE¼), 1952 m, 15 Sept 1982, *E. Evert 4999*, MOR, RM. First reports for Wyoming.

ROSACEAE

Sanguisorba minor **Scop.** Wyoming, Sheridan Co., Wildlife Refuge ca 5 km W of Dayton, 1403 m, 30 Jun 1979, *R. Hartman 9873*, RM. Park Co., along Rt. 14 at Blackwater Picnic area (T52N R107W S21 SW¼), 1882 m, 27 Jun 1982, *E. Evert 4033*, RM. First reports for Wyoming.

LITERATURE CITED

DORN, R. D. 1977. Manual of the vascular plants of Wyoming. Garland Publishing Inc., New York.

LOFGREN, L. C. 1956. Alpine flowering plants of the Cloud Peak–Cliff Lake area, Bighorn County, Wyoming. Unpublished thesis. University of Wyoming, Laramie.

ON *COWANIA* AND ITS INTERGENERIC HYBRIDS IN ARIZONA[1]

Marc A. Baker[2], Donald J. Pinkava[2], Bruce Parfitt[2], and Timothy Righetti[3]

ABSTRACT.— The putative intergeneric hybridization between Stansbury Cliffrose (*Cowania*) and Apache Plume (*Fallugia*) is found to be undocumented. Chromosome counts support reported base numbers for *Cowania* and *Fallugia* to be $n = 9$ and $n = 14$ respectively.

In 1975, Blauer et al. reported the existence of a small population of putative hybrids between Stansbury Cliffrose (*Cowania mexicana* D. Don var. *stansburiana* [Torr.] Jeps.) and Apache Plume (*Fallugia paradoxa* [D. Don] Endl.) (Rosaceae). The putative hybrids occurred with both proposed parental taxa along Ranger Pass, about 20 km west of Big Springs Ranger Station in the Kaibab National Forest, Coconino County, Arizona. This appears to be the only published report of natural hybridization between these taxa.

In 1981, Righetti made a collection from the most robust of three putative hybrid individuals composing the original population. The flowers have two series of sepal-like bracts (characters of Apache Plume) and numbers of pistils per receptacle intermediate to those of the proposed parents. However, the plant has glandular involucres, vegetative characters, and nitrogen-fixing properties that characterize Stansbury Cliffrose.

The following spring, Baker collected buds from this same robust plant to obtain a microsporogenic count. No stamens were found; indeed the plant has only pistillate flowers. To our knowledge, Stansbury Cliffrose always has perfect flowers, but pistillate plants have been reported for Apache Plume (Blauer et al. 1975). Root tips from several vegetative cuttings propagated by Righetti as a part of a nitrogen fixation study (Righetti et al. 1983) have yielded a mitotic count of $2n = 18$ (Table 1), the same number known for Stansbury Cliffrose. Meiotic counts of Apache Plume, including one individual collected near the putative hybrid are $n = 14$ (Table 1), in agreement with six counts independently obtained by McArthur et al. (1983) for Utah, Arizona (Pipe Springs, Mohave County), and Texas, all in disagreement with the first and only other count of $2n = 18$ by Baldwin (1951), apparently in error.

Blauer et al. (1975) reported that, from 72 seeds collected from this population in 1968, 16 (22.2%) germinated and only 2 survived to young plants. Artificial crosses between the two putative parent taxa produced 1,418 seeds, of which 47 (3.3%) germinated and 7 survived using Stansbury Cliffrose as the maternal plant; 3,647 seeds, of which 19 (0.5%) germinated and none survived using Apache Plume as the maternal parent. However, no detailed evidence for hybridization was given and no seedlings are extant. Hybrid seedlings would be expected to have characters intermediate to the putative parents and a chromosome count of $2n = 23$ (14 from Apache Plume and 9 from Stansbury Cliffrose). In 1981, Righetti collected from the same robust putative hybrid approximately 40,000 seeds, of which about 150 were deemed likely to germinate. Nine seeds germinated and 7 are live seedlings. All 7 seedlings have vegetative characters and chromosome count ($2n = 18$) attributable to Stansbury Cliffrose.

We conclude that the putative hybrid plant in question is a diploid, aberrant, pistillate plant of Stansbury Cliffrose, in which the stamens have converted to pistils or pistil-

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lodes (many being sterile, some with seeds exposed through walls of the pistillodes) and the petals have become sepaloid (involucral bracts, as in Apache Plume, being absent). The two other putative hybrid individuals succumbed to a fire in the winter of 1981. The robust individual we tested was badly damaged in the same fire and did not survive the winter of 1982. Thus, no natural hybrids between these taxa have been documented.

A second intergeneric hybrid, *Purshia glandulosa* Curran, often recognized as a species, is believed to have arisen via allopatric introgression of Stansbury Cliffrose genes into Bitterbrush (*Purshia tridentata* (Pursh) DC. (Thomas 1957). This putative hybridization supposedly took place at the end of the Pleistocene pluvial period, when mountain ranges were still being uplifted, and resulted in hybrid populations better adapted to the shorter growing seasons caused by increasing altitude and more arid summers (Stebbins 1959). Stutz and Thomas (1964) argue for recent stepwise introgression of characters of *Cowania* from one population to the next northward several hundred miles of the current range of *Cowania. Purshia glandulosa* has been reported for northern Arizona by Stebbins (1959, outline map), Blauer et al. (1975), Koehler and Smith (1981, map), Welsh (1982), and McArthur et al. (1983), but all references are without specimen citation. We document its occurrence in Arizona with a collection by Ralph Gierisch (*Gierisch 4714*, ASU), from near Whitney Pass, Mohave County. Hybrids between *P. glandulosa* and Stansbury Cliffrose have been reported from eastern California (Koehler and Smith 1981), but no hybrids between these taxa are known from Arizona.

Cowania subintegra Kearney is known only from two isolated populations, both in Arizona: near Bagdad (Mohave County) and near Bylas (Graham County). Chromosome counts ($n = 9$) have been obtained from both populations, the former by McArthur et al. (1983) and the latter by Parfitt (Table 1).

TABLE 1. Chromosome counts of *Cowania* and *Fallugia* taxa in Arizona. Voucher specimens deposited in ASU.

Cowania mexicana D. Don var. *stansburiana* (Torr.) Jeps.	
$n = 9$	Coconino Co.: Ranger Pass, ca 20 km W of Big Springs Ranger Sta., T37N, R2W, S27, *Righetti 5*.
	Yavapai Co.: Rt. I-17, 1.1 km S of jct. Rt. 293 at McGuireville, T14N, R5E, S4, *Righetti 25*.
$2n = 18$	Coconino Co.: Rt. 89A, ca 20 km E of Jacob Lake, T39N, R3E, S34, *Righetti 3*; Ranger Pass, ca 20 km W of Big Springs Ranger Sta., T37N, R2W, S27, *Righetti s.n.* (cutting from aberrant pistillate plant).
Cowania subintegra Kearney	
$n = 9$	Graham Co.: US70, ca 18 km NW of Bylas, *Clark 1506 & Parfitt*.
Fallugia paradoxa (D. Don) Endler	
$n = 14$	Coconino Co.: Painted Desert Vista, Sunset Crater Loop Rd. 545, T23N, R9E, S9, *Righetti 11, 12*; Rt. 89A, ca 20 km E of Jacob Lake, T39N, R3E, S34, *Righetti 7*; Ranger Pass, ca 20 km W of Big Springs Ranger Sta., T37N, R2W, S26, *Baker 4377 & Trushel*.
	Yavapai Co.: Rt. I-17, ca 0.8 km S of milepost 303; T15N, R6E, S3, *Righetti 9*.

LITERATURE CITED

BALDWIN, J. T. 1951. Chromosomes of *Spiraea* and of certain other genera of Rosaceae. Rhodora 53:203–206.

BLAUER, A. C., A. P. PLUMMER, E. D. MCARTHUR, R. STEVENS, AND B. C. GIUNTA. 1975. Characteristics and hybridization of important intermountain shrubs. I. Rose Family. USDA Forest Service Research Paper INT-169:1–36.

KOEHLER, D. L., AND D. M. SMITH. 1981. Hybridization between *Cowania mexicana* var. *stansburiana* and *Purshia glandulosa* (Rosaceae). Madroño 28:13–25.

MCARTHUR, E. D., H. C. STUTZ, AND S. C. SANDERSON. 1983. Taxonomy, distribution, evaluation, and cytogenetics of *Purshia, Cowania,* and *Fallugia* (Rosoideae, Rosaceae). Pages 4–24 *in* K. L. Johnson and A. P. Tiedemann, eds., Research and management of Bitterbrush and Cliffrose in western North America. Proceedings of Symposium, Salt Lake City, Utah. Gen. Techn. Rep. INT., 152, USDA, U.S. Forest Service, Intermountain Forest and Range Experimental Station, Ogden, Utah. 279 pp.

RIGHETTI, T. L., C. H. CHARD, AND D. N. MUNNS. 1983. Opportunities and approaches for enhancing nitrogen fixation in *Purshia, Cowania,* and *Fallugia.* Pages 214–224 *in* K. L. Johnson and A. P. Tiedemann, eds., Research and management of Bitterbrush and Cliffrose in western North America. Proceedings of Symposium, Salt Lake City, Utah.

Gen. Techn. Rep. INT., 152, USDA, U.S. Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah. 279 pp.

STEBBINS, G. L. 1959. The role of hybridization in evolution. Proc. Amer. Philos. Soc. 103:231–251.

STUTZ, H. C., AND L. K. THOMAS. 1964. Hybridization and introgression in *Cowania* and *Purshia*. Evolution 18:183–195.

THOMAS, L. K. 1957. Introgression in *Purshia tridentata* (Pursh) DC. and *Cowania stausburiana* Torr. Unpublished thesis. Brigham Young Univ., Provo, Utah. 66 pp.

WELSH, S. L. 1982. Utah flora: Rosaceae. Great Basin Nat. 42:1–44.

AN ECOLOGICAL STUDY OF BRISTLECONE PINE (*PINUS LONGAEVA*) IN UTAH AND EASTERN NEVADA[1]

R. D. Hiebert[2] and J. L. Hamrick[3]

Abstract.— This paper presents data on the distribution of *Pinus longaeva* on the Markagunt Plateau, Utah; and the Snake, Egan, and White Pine ranges of eastern Nevada. It also presents data on the present-day density and age structure of three *P. longaeva* populations and the growth rates of individual trees within these populations.

Conifer species richness and the relative abundance of *P. longaeva* varies clinally from the Markagunt Plateau to the White Pine Range. The Markagunt Plateau has relatively high conifer species richness (10 species) and low relative abundance of *P. longaeva* (1%). The White Pine Range has low conifer richness (4 species) and high *P. longaeva* relative abundance (34%). Individual tree growth rates were low but highly variable in all populations studied. The three populations studied had mixed age structures with a general trend of more younger individuals at the lower elevations.

Possible explanations for the present distribution of *P. longaeva* and the population structures observed are discussed.

The distribution and abundance of a species results from the interaction of several environmental parameters. Innate factors such as nutrient and moisture requirements, vegetative growth rate, and age to first reproduction interact with and are influenced by physical and biotic factors of the environment. If the ecology of a species is to be understood, the relative influence of these and other parameters on its distribution and abundance must be determined. Without this information, predictions about the future health and dynamics of poulations cannot be made. Such predictions are especially difficult for long-lived species whose population dynamics cannot be followed over time. For such species present-day characteristics of its population such as density, age structure, and individual growth rate must be used to describe past fluctuations in population size, to evaluate the present status of the population, and to predict future growth or reduction in population numbers. Such analyses may be especially valuable in devising management plans for rare or endangered species.

This paper represents a study of the ecology of four bristlecone pine (*Pinus longaeva*) populations located on selected mountain ranges in Utah and Nevada. It describes the distribution of bristlecone pine in western Utah and eastern Nevada and attempts to document, by use of present-day densities, age structure, individual growth rates, and spatial and temporal fluctuations within these stands. *Pinus longaeva* was selected for study due to its great longevity, its interesting biogeographical distribution, and the existence of relatively undisturbed stands.

Species Description.

Based on morphological considerations, Bailey (1970) split bristlecone pine into two species. The Colorado and New Mexico populations retained the name *Pinus aristata* Engelm., and populations west of the Colorado River were designated *Pinus longaeva* Bailey (Bailey 1970). Subsequent studies of the terpenoid chemistry and crossability of the two forms provided further support for two species (Mastroguiseppe 1976, Zavarin et al. 1973, 1976, Critchfield 1977). The latter species, *Pinus longaeva*, is the subject of this study.

Pinus longaeva is generally found at high altitudes, often extending to timberline on

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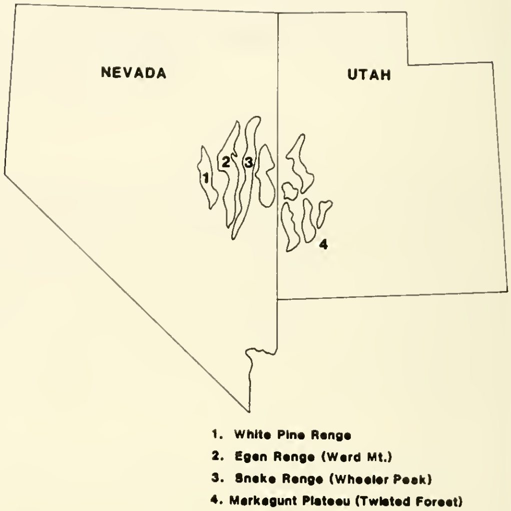
the mountain ranges of Utah and Nevada and the White Mountains of eastern California. It is typically localized in areas with poor soils but may also form extensive stands. Isolated trees can be found on mesic sites with sufficient sunlight (Wright and Mooney 1965, Beasley 1980). On these sites, *P. longaeva* has a fast-growing, erect growth form instead of the twisted, gnarled, slow-growing form that predominates on poor sites. It has also been observed to form krumholtz at its upper elevational limits. One of the best known and most interesting characteristics of *P. longaeva* is its great longevity, as it attains ages approaching 5,000 years (Currey 1968, Ferguson 1968).

The present distribution of *P. longaeva* in the Great Basin is on isolated mountain ranges separated by xeric valleys of sagebrush and shadscale. At the higher elevations the environment of these ranges is more favorable, with some ranges supporting diverse communities of montane conifers. The most eastern ranges are generally more mesic since precipitation in the Great Basin decreases to the west. Perhaps as a result, the number of conifer species decreases from 10 on the eastern ranges to as few as 2 on the most western ranges (Critchfield and Little 1966). Associated with the decrease in conifer species richness is an increase in the relative abundance, size of stands, and altitudinal range of bristlecone pine.

We are aware of no studies of the population ecology of *P. longaeva*. Previous studies of bristlecone pine have been concerned with the establishment of paleoclimatic records through the use of dendrochronology techniques (Ferguson 1970c, Fritts 1965, LaMarche et al. 1974, Wilson and Grinstad 1975) and with the ecological physiology of this species. Eco-physiological studies have generally focused on finding explanations for its tolerance to extreme habitats and great longevity (Schulman 1954, Fritts 1965, LaMarche 1969, Mooney et al. 1966, Schultze et al. 1967, Wright et al. 1965, Beasley et al. 1971). Recently we (Hiebert and Hamrick 1983) published genetic data that was consistent with what is known of the recent paleoecological history of *P. longaeva* in the Great Basin (Wells 1983). We observed high genetic variations within populations and low genetic variation between populations. Paleoecological studies have shown bristlecone pine to form large contiguous populations throughout much of the Great Basin during glacial episodes during the last 40,000 years.


NEVADA
UTAH
1
2
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1. White Pine Range
2. Egan Range (Ward Mt.)
3. Snake Range (Wheeler Peak)
4. Markagunt Plateau (Twisted Forest)

Fig. 1. Locations of mountain ranges and *Pinus longaeva* populations included in this study.

STUDY SITES

The population ecology of *P. longaeva* was investigated on four mountain ranges in Utah and eastern Nevada. The ranges included from east to west the Markagunt Plateau (north rim of Cedar Breaks) in Utah, and the Snake, Egan, and White Pine ranges of eastern Nevada. Three populations were selected for more detailed ecological studies: Twisted Forest (TF), Markagunt Plateau; Wheeler Peak (WP), Snake Range; and Ward Mountain (WM), Egan Range (Fig. 1). Twisted Forest and Ward Mountain stands occur on limestone substrate, and the Wheeler Peak population is on quartzite glacial till. The population at Wheeler Peak is located on a west- to northwest-facing slope at an elevation of 3250–3500 m. The other two populations range between 2700 and 3200 meters in elevation. Most of the population at

Twisted Forest is a monospecific stand of *P. longaeva.* The understory is completely bare except for a dwarfed *Castilleja* (Indian paintbrush) species. However, at the lower boundary of the population (a stream bed), bristlecone pine is associated with *Pinus flexilis, Picea englemannii,* and *Pseudotsuga menziezii.* In the Wheeler Peak population, bristlecone pine shares dominance with *P. engelmannii* and *P. flexilis.* The lower edge of the population drops into a mesic canyon, where vegetation is dominated by a dense stand of *P. englemannii.* On Ward Mountain, bristlecone pine is associated with *P. engelmannii* on north-facing slopes and with *P. flexilis* on the more open, exposed sites. The understory there is dominated by *Artemisia tridentata.*

METHODS

Montane and subalpine conifer species richness, relative abundance, and dispersion were obtained for each mountain range by establishing altitudinal transects extending along equivalent compass points from the highest peak or timberline to the lower boundary of the montane conifer zone. Every tree within 5 m of the transect was tallied, and observations were made on the topography and soils of those habitats where bristlecone pine occurred.

To estimate population parameters for the three bristlecone pine stands, two or three vertical line transects and two horizontal line transects were subjectively chosen. The point-quarter method of Cottam and Curtis (1956) was employed to sample bristlecone pine at 100–150 m intervals. The sample consisted of 24 points/population. Sample trees were tagged, DBH measured, height estimated, and one radial core was taken at breast height (4½ feet) using a 40-cm increment core. The cores were mounted on grooved boards in the field and returned to the laboratory for counting.

Increment cores were polished, and the number of growth rings along one radius was counted using a binocular microscope. Due to short growing seasons at high altitudes, there was little difficulty with false growth rings. When a complete core to the center of a tree was obtained, the number of rings was assumed to represent the minimum age of the tree. For trees with incomplete radial cores, total age was estimated. Trees of known age and diameter were used to estimate ages of trees with incomplete cores for which actual tree average growth rates and diameters were known. Growth rates of the individual trees gave the best estimate of age, with correlation coefficients ranging from 0.89 to 0.95 for the three populations. The accuracy of this prediction was best for large trees whose ages we were most interested in estimating. Thus, for trees with incomplete radial cores, a core of 40 cm was obtained, the rings counted, and the average growth rate determined. The average growth rate of the tree was then used to estimate the number of growth rings in the uncored radius.

Population densities were calculated using standard point-quarter techniques (Cottam and Curtis 1956). The average increase in DBH/year was determined by dividing the diameters of the trees by their age.

Size structure of the populations was determined by calculating the frequency of trees within 20-cm diameter classes. Age classes were set at 250-yr intervals.

Mean ages were also calculated and the Student-t-test applied to determine whether significant differences occurred among populations, or among different areas within populations.

RESULTS

Montane and subalpine conifer species richness and the relative abundance of *P. longaeva* varies clinally from the Markagunt Plateau to the White Pine Range (Table 1). Montane and subalpine conifer species richness is relatively high on the Markagunt Plateau (10 species) and the Snake range (8 species) but is lower on the more western Egan and White Pine ranges (5 and 4 species). Associated with the decrease in conifer species diversity from east to west is an increase in the relative abundance and altitudinal range of *P. longaeva* (Fig. 2). *Pinus longaeva* is usually restricted to poor edaphic conditions on the Markagunt Plateau and the Snake Range and has correspondingly abrupt

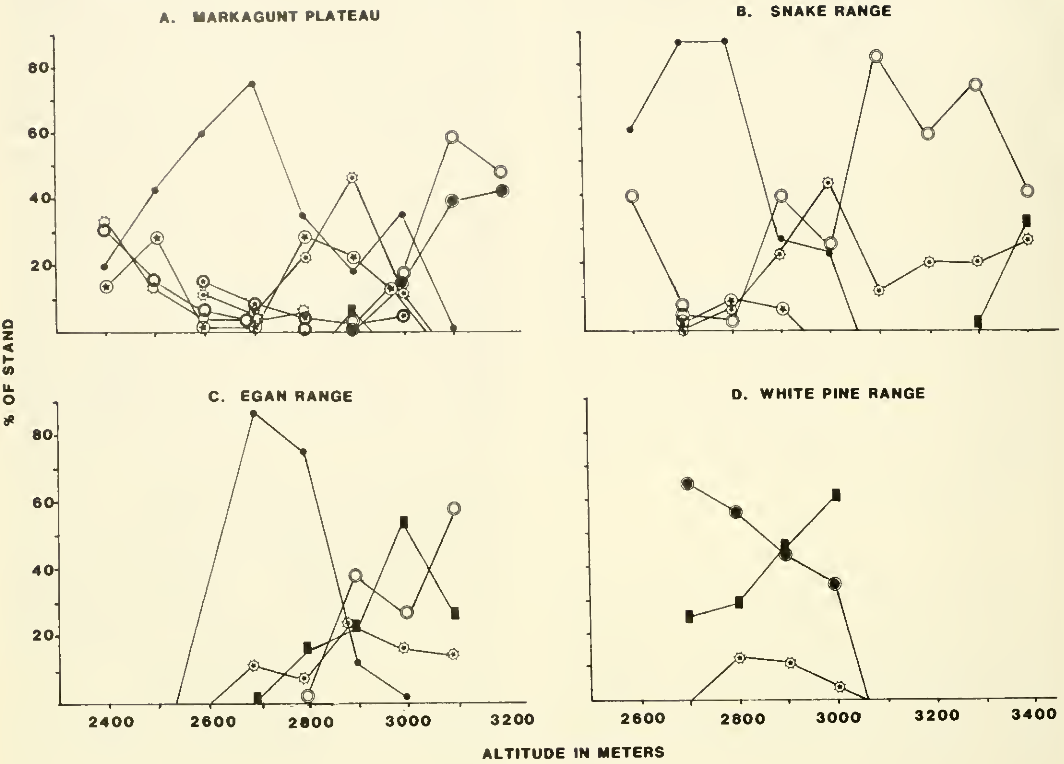

Fig. 2. The relative abundance of montane and subalpine conifers along an altitudinal gradient on the Markagunt Plateau of Utah and three eastern Nevada ranges. Key to species: *Abies concolor* ● (white fir), *A. lasiocarpa* ⬤ (subalpine fir), *Juniperus scopulorum* ✪ (Rocky Mountain juniper), *Picea engelmannii* ◎ (Engelmann spruce), *Picea pungens* ⊛ (blue spruce), *P. flexilis* ❂ (limber pine), *Pinus longaeva* ▮ (bristlecone pine), *P. ponderosa* ○ (ponderosa pine), *Pseudotsuga menziesii* ⊛ (Douglas fir).

population boundaries. Individual trees can be found at a wide variety of habitats, however. Stands on the Egan and White Pine Ranges are larger, have a broader altitudinal range, and stand boundaries are less abrupt. Stands here are found to exist on mesic as well as poor edaphic sites.

Estimates of the numbers of individuals per stand and their densities are given in Table 2. Population numbers are high, but densities are low in comparison to more mesophytic conifer stands. Comparisons of densities between populations indicate that WP and WM are similar, but that the density of TF is over twice that of the other two populations. This would appear to be due, at least in part, to the monospecific nature of this population, but may also be due to different physical conditions. Population densities are not homogeneous among elevation zones (Table 2). Each population has its highest densities at the lower elevations.

Growth rates of individual trees can be used as an indicator of overall environmental hospitality. Beasley (1980) found that bristlecone pine grows best on sites with favorable moisture conditions. However, in these three populations the growth rates of bristlecone pine are low (Table 3). Comparisons among populations indicate that the growth in diameter in WP and TF were effectively equal. On Ward Mountain, however, where bristlecone pine is assumed to be found on a wider variety of sites, mean growth rates are significantly higher ($p < .001$). If growth rates are a good indicator of habitat hospitality, WP has the harshest environment, followed closely by TF.

Table 1. Species richness and relative abundances of montane and subalpine conifers on selected ranges in Utah and Nevada.

Species	Relative abundance (%) Markagunt Plateau	Snake Range	Egan Range	White Pine Range
Abies concolor	34	31	40	54
A. lasiocarpa	11	—	—	—
Juniperus scopulorum	5	1	—	—
J. communis	0*	2	1	6
Picea engelmannii	15	34	19	—
P. pungens	4	—	—	—
Pinus flexilis	13	23	16	6
P. longaeva	1	1	24	34
P. ponderosa	5	1	—	—
Pseudotsuga menziesii	12	8	—	—
Total species	10	8	5	4

*Present but less than 1%

Populations TF and WM have similar patterns of individual growth at different elevations within populations, but the pattern in WP differs. Growth rates at the lower elevations of TF and WM are significantly higher ($p < .01$) than those of the middle and upper elevations. This comparison is valid because the growth rates of small and large trees are not significantly different. These results indicate that the lower elevations offer the most hospitable environments.

Tree size (DBH) is often used as an indicator of age. However, since direct estimates of age were obtained from counting growth rings, the size data is not presented. Also, although DBH is significantly correlated ($p < .01$) with age in bristlecone pine, it explains only 70% of the total variation in age. All populations have a mixed size structure with a high proportion of small individuals. This indicates that these forest stands are reproducing themselves (Wikam and Walli 1970).

Table 2. Densities (trees/ha) and approximate numbers of individuals of three bristlecone pine (*Pinus longaeva*) populations in Utah and Nevada.

	Twisted Forest (TF)	Wheeler Peak (WP)	Ward Mt. (WM)
Altitudinal zone			
Upper	138	57	51
Middle	138	99	94
Lower	224	75	102
Population mean	163	72	77
Number of individuals	17,000	8,500	14,000

Populations TF and WM have age structures strongly skewed toward the younger age classes. In the absence of any signs of disturbance by man or of any widespread catastrophic events, the age structures suggest an increase in population numbers. The age distribution of WP is indicative of a stationary population. It should be noted that the age structure of WM has certain age classes with few or no trees. This could represent periods of low recruitment or could be an artifact of the sample size. Age classes with few representatives correspond to cool-dry climatic periods at approximately 900 and 2500–3000 years B.P., respectively (LaMarche 1974).

The mean ages of trees in the three elevational zones from population TF are significantly different ($t = 2.274$ to 5.633; $p < .01$). The average ages of the high and low ($t = 7.916$; $p < .001$) and the middle and lower portions ($t = 4.218$; $p < .001$) of WM are also significantly different. In contrast, the mean age of trees from the three altitudinal zones within WP were not significant, although the age distributions do not appear to be equivalent.

TF and WM have similar patterns of variation in age structure along the altitudinal gradient. A low proportion of young trees and a high proportion of old trees are observed at the upper elevations, a condition that is indicative of decreasing or stationary population numbers. The intermediate elevations have higher proportions of young trees, but several old trees are also present, in-

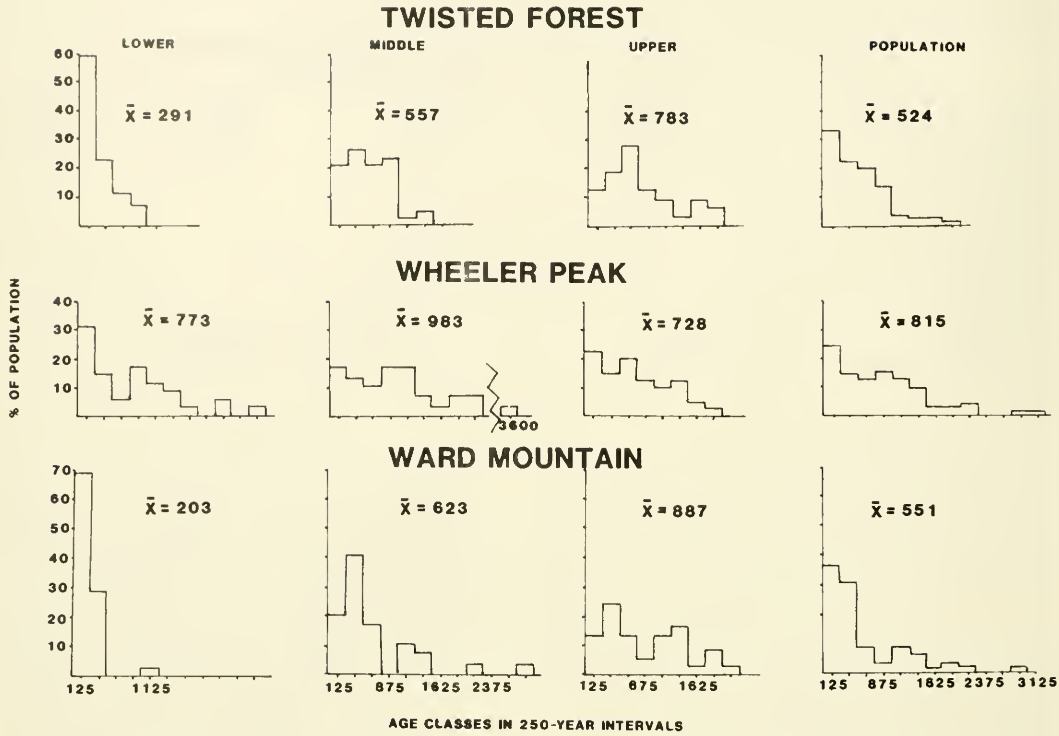

Fig. 3. The age distribution of three *Pinus longaeva* populations in Utah and Nevada. Mean ages and the age distribution at three different altitudes within each population are also given. The age classes are in 250-year intervals.

dicating that population size in the middle zone is either stationary or growing slowly. The presence of many old trees also indicates that bristlecone pine has occupied these areas for some time. The lower portions of these two populations have age distributions strongly skewed toward the younger age classes, with no trees over 1100 years in age.

Population WP does not fit this pattern in all respects, but the age distributions at different altitudes indicate (Fig. 3) that the greatest establishment is presently occurring at lower elevations. Due to the presence of many old trees, the age distribution at the lower portion of this population is not indicative of a newly colonized site.

The method of Leak and Graber (1974) was applied to the data to test whether bristlecone pine stands are spreading into the lower elevations. This method is based on the premise that population spread is reflected in the relationship of maximum and minimum ages of the trees in the stand. The maximum age should be old and the minimum age

Table 3. Average growth rates of trees in DBH in three bristlecone pine (*Pinus longaeva*) populations in Utah and Nevada. Growth rates of trees at different altitudes within populations are also compared. N = the number of trees sampled. Increase in DBH is in mm/yr.

	Twisted Forest	N	Wheeler Peak	N	Ward Mt.	N
Increase in diameter/yr°						
Population mean	.864	112	.725	101	1.226	110
Upper	.701	33	.834	37	.963	37
Middle	.645	38	.637	29	1.021	30
Lower	1.200	41	.673	41	1.700	43

°Growth rates of populations or altitude classes connected by lines are not significantly different as determined by the student-t-test. Those not connected are significantly different.

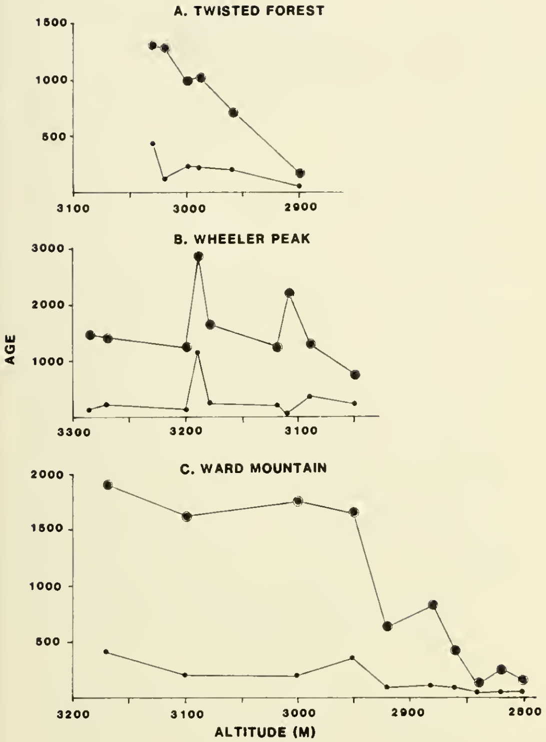

Fig. 4. The age of the oldest and youngest trees along an altitudinal gradient. This method is used to detect migration of forest vegetation (Leak and Graber 1974). Small dots = minimum age. Large dots = maximum age.

young if the population is static in the area. If both the maximum and minimum tree ages are young, the area probably has been recently colonized.

At the higher altitudes of TF (Fig. 4) the maximum and minimum tree ages are old, indicating an old, poorly reproducing stand. The center of this population is static, but the lower portion of the population appears to be recently colonized. The plots (Fig. 4) for WP are not smooth and as a result are harder to interpret. Generally, it appears that the extreme lower portion of the population is a relatively young, newly established stand. Population WM appears to be static at the upper and middle zones, but has only recently become established below 2900 m.

Discussion and Conclusions

The distribution of *Pinus longaeva* on these mountain ranges is strongly associated with species richness of montane and subalpine conifers. Where conifer species richness is relatively high on the Markagunt Plateau and the Snake Range, *P. longaeva* stands are restricted to poor edaphic sites and have abrupt boundaries. On the Egan and White Pine ranges, where conifer species richness is relatively low, the area, altitudinal range, and types of habitats dominated by *P. longaeva* are greatly increased. Why conifer species richness decreases from east to west in the Intermountain Region is subject to debate. It is possible that some conifer species have not had the time or dispersal ability to become established on the middle and western Great Basin ranges (Wells 1983). Alternatively, their ranges may be restricted because environmental conditions are suboptimal or intolerable. The western ranges are more xeric than the eastern ranges due to the rain shadow of the Sierra Nevada of eastern California.

Bristlecone pine is probably absent from the mesic sites (high moisture and nutrient availability) due to its low shade tolerance (Baker 1950). On harsh sites, where it is released from competition for light, it is able to form stands because of its low nutrient and moisture requirements (Beasley and Leemredson 1980). The increased dominance of *P. longaeva* on the Egan and White Pine ranges may result from the suboptimal or intolerable conditions for more mesophytic species such as *Picea engelmannii*. This explanation could be tested by detailed studies of fossil material in woodrat middens dating to the Holocene in the area, coupled with detailed measurements of soil and nutrient levels in the field and testing of relative tolerance ranges for the conifer species involved.

Growth rates of individual trees are slow but highly variable within and among stands, demonstrating the sensitivity of *P. longaeva* to its environment. It is this sensitivity that has made *P. longaeva* so valuable in the reconstruction of past climatic events (LaMarche 1974). The present age structure of these three populations indicates they are maintaining or increasing their numbers. Furthermore, the elevational pattern of age distributions within populations indicates a downward shift in the altitudinal range of *Pinus longaeva* over the last few hundred years. Obviously, the spatial distribution and abundance of *P. longaeva* on these mountain ranges has varied through time.

Literature Cited

Bailey, D. K. 1970. Phytogeography and taxonomy of *Pinus* subsection Balfourianae. Ann. Missouri Bot. Gard. 57:210-249.

Baker, F. S. 1950. Principles of silviculture. McGraw Hill, New York.

Beasley, R. S., and J. O. Klemnedson. 1980. Ecological relationships of bristlecone pine. Amer. Midl. Nat. 104:242-252.

Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology 37:451-460.

Critchfield, W. B. 1977. Hybridization of foxtail and bristlecone pines. Madroño. 24:193-211.

Critchfield, W. B., and E. L. Little, Jr. 1966. Geographical distribution of the pines of the world. USDA Misc. Publ. 991. 97 pp.

Currey, D. R. 1968. An ancient bristlecone pine stand. Ecology 44:564-566.

Ferguson, C. W. 1968. Bristlecone pine: science and esthetics. Science 159:839-846.

______. 1970. Dendrochronology and bristlecone pine in east-central Nevada. Terminal report submitted to the regional forester. U.S. Forest Service, Ogden, Utah. 56 pp.

Fritts, H. C. 1965. Tree-ring evidence for climatic changes in western North America. Mon. Weather Rev. 93:421-443.

______. 1966. Growth rings of trees: their correlation with climate. Science 154:973-979.

Hiebert, R. D., and J. L. Hamrick. 1983. Patterns and levels of genetic variation in Great Basin bristlecone pine, *Pinus longaeva*. Evolution 37:302-310.

LaMarche, V. C. 1969. Environment in relation to age of bristlecone pines. Ecology 50:53-59.

______. 1974. Paleoclimatic inferences from long tree-ring records. Science 183:1043-1048.

LaMarche, V. C., and H. A. Mooney. 1967. Altithermal timberline advance in western United States. Nature 213:980-982.

Leak, W. B., and R. E. Graber. 1974. A method for detecting migration of forest vegetation. Ecology 55:1425-1427.

Mastroguiseppe, J. D. 1976. Flavonoids of *Pinus* subsection Belfourianae. Bot. Soc. Amer. Annual Meeting. Abstract of Papers:57-58.

Mooney, H. A., M. West, and R. Brayton. 1966. Field measurements of the metabolic responses of bristlecone pine and big sagebrush in the White Mountains of California. Bot. Gaz. 127:105-113.

Schulman, E. 1954. Longevity under adversity of conifers. Science 119:1396-1399.

Wells, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecol. Monogr. 53:341-382.

Wikam, D. A., and M. K. Wali. 1974. Analysis of a North Dakota gallery forest: vegetation in relation to topographic and soil gradients. Ecol. Monogr. 44:441-464.

Wilson, A. T., and M. J. Grinsted. 1975. Paleotemperatures from tree rings and the deuterium hydrogen ratio of cellulose as a biochemical thermometer. Nature 257:387-388.

Wright, R. D., and H. A. Mooney. 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains of California. Amer. Midl. Nat. 73:257-284.

Zavarin, E., and K. Snajberk. 1973. Variability of wood monoterpenoids from *Pinus aristata*. Biochem. Syst. 1:39-44.

Zavarin, E., K. Snajberk, and D. Bailey. 1976. Variability in the essential oils of wood and foliage of *Pinus aristata* and *Pinus longaeva*. Biochem. Syst. 4:81-92.

BURROWING AND DENNING HABITS OF A CAPTIVE COLONY OF THE UTAH PRAIRIE DOG

Harold J. Egoscue[1] and Elizabeth S. Frank[2]

Abstract.— Burrows, hibernaculums, and nests of an exhibit colony of the Utah prairie dog, *Cynomys parvidens*, are described.

Little has been published about the burrowing and denning habits of white-tailed prairie dogs (Subgenus *Leucocrossuromys*). Longhurst (1944) described and diagrammed four burrows of *Cynomys* g. *gunnisoni*, which contained no hibernating animals, and Clark (1977) described two burrows of *C. leucurus*, one of which was only partially excavated but thought to contain a hibernating prairie dog. As noted by Pizzimenti and Collier (1975), the burrows of the Utah prairie dog, *C. parvidens*, have not been investigated.

Methods

An earth-filled, circular, fenced enclosure 14.6 m in diameter containing a colony of seven Utah prairie dogs at the National Zoological Park, Washington, D.C., was excavated in October and November 1978 after the animals had become completely inactive aboveground. A concrete footing that extended almost 2.75 m belowground and an unmortared brick bottom provided drainage but prevented the animals from burrowing out.

Utah prairie dogs had occupied the exhibit since 1971; their numbers varied from 6 to 18 animals (average about 8). At least seven litters of young were raised. The 1975 crop of 10 young was sent to Hogle Zoological Garden, Salt Lake City, Utah; otherwise all young were left in the colony.

Excavation was done in two stages: (1) by digging along the burrows until all that could be located were uncovered and mapped, and (2) by carefully removing the remaining dirt, mostly by pick and shovel, until all animals were found.

Results and Discussion

The entrances and upper level tunnels shown in Figure 1 represent the cumulative efforts of several generations of animals over 7.5 years of habitation. There were two types of burrows: (1) deep, permanent, usually but not always interconnected systems many meters long, with several entrances, nest chambers, and "turn-arounds" (near some but not all entrances), where the occupants slept, reared young, sought shelter, and hibernated; and (2) short, shallow, usually unbranched tunnels open at both ends, and less than 1.8 m long that seemed to be used mainly for emergency hiding places. Although some of the latter were maintained in good repair for more than a year, none was enlarged into a main burrow or subsequently became part of an existing main burrow. All these simple burrows were located close to or against the concrete footing and may have represented artifacts of captivity.

None of the upper-level tunnels shown in Figure 1 led to hibernaculums. Apparently passages to deeper levels where the hibernating animals were later discovered were plugged, probably where they branched from the shallower levels and were overlooked. Three chambers containing old nests in varying stages of decay were located at the ends of short unplugged side tunnels 46–61 cm off main tunnels and at depths of 61, 71, and 79 cm below ground level. Two of these measured about 25 x 25 x 28 and 25 x 20 x 25 cm and were almost globular. Since all were at or above the frost line (about 76.2 cm below the surface in this part of Washington,

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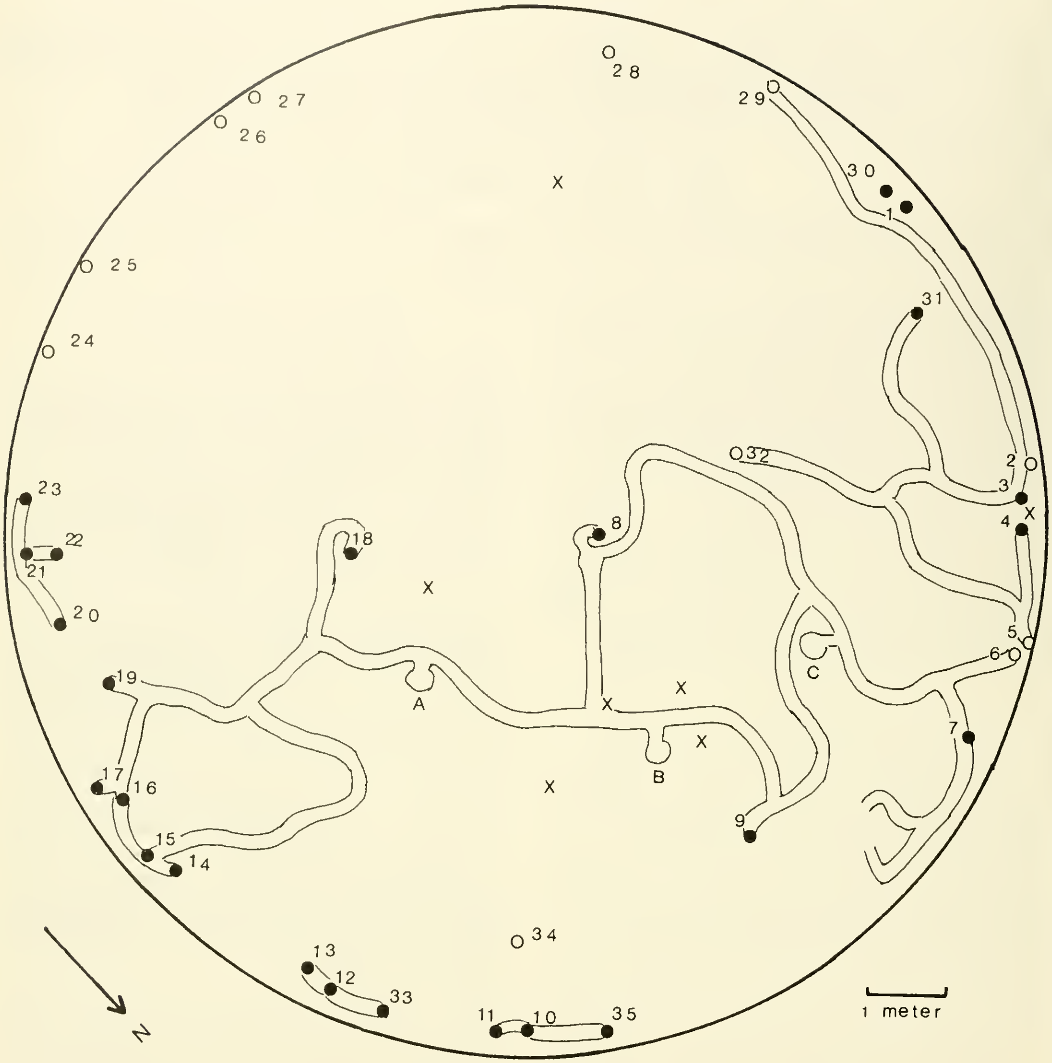

Fig. 1. Diagram of Utah prairie dog enclosure showing (1) den entrances (solid circles = active entrances, open circles = inactive and abandoned entrances); (2) all upper-level burrows (width not to scale); (3) locations of nests in upper-level burrows (capital letters); and (4) positions of nests at deeper levels where hibernating animals were found (X's). Diameter of enclosure was 14.56 m.

D.C.), it was assumed they were not used for hibernation.

Nests occupied by hibernating animals were found 107, 122, 135, 142, and 208 cm below the surface. The smallest chamber measured 22 x 24 x 24 and the largest 28 x 25 x 30 cm. Each was filled to capacity with dry plant material (Fig. 2) gathered from the surface. The innermost materials in contact with the occupant's body were finely shredded. The dirt below each nest was dry and powdery to a depth of about 2 cm and slightly warm to the touch. The deepest hibernaculum was about 0.6 m from the bottom. We found no tunnels or nests in contact with the bricks. The nests contained no fecal material or ectoparasites.

When located, two of the seven animals were completely inactive, three were in early stages of arousal but still in their nests and unable to make coordinated movements, and the last two were not only fully awake but also sought to evade capture. Our prolonged digging activities may have aroused the latter

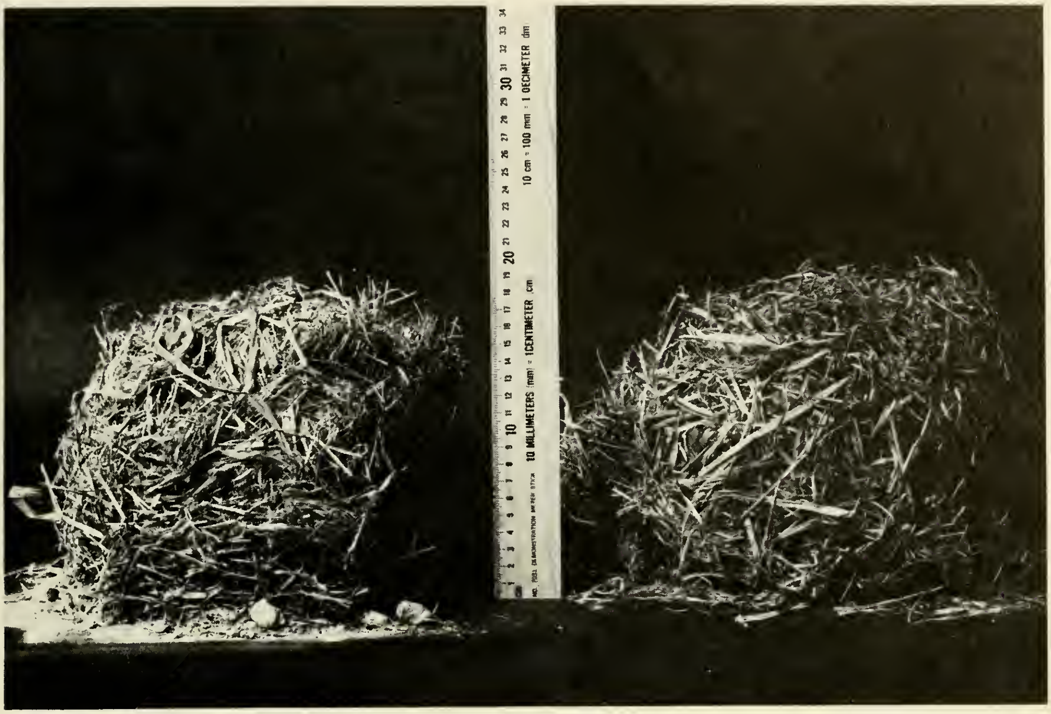

Fig. 2. Nests of the Utah prairie dog. Scale in mm (Photo by S. Baronh).

two individuals. All hibernating animals nested separately. The closest two occupied nests were about 1.2 m apart at approximately the same depth.

Of the 35 entrances shown in Fig. 1, 24 were active in 1978, but only about half of these led to main burrows. Other active entrances (e.g., 35, 10, 11, 33, 12, and 13) were to "emergency hiding" burrows. Old entrances 24–25 and 26–27 marked the ends of two such burrows that were active from 1972 to 1975 and then abandoned. Old entrance 34 originally led to a main burrow system and was used from 1973 to the summer of 1975, when heavy rains filled it with soil, and it was never reopened. Entrance 18 marked the location of the first burrow dug by the wild-trapped stock in 1971 and was the only entrance in continuous use for the entire history of the colony. It was also the entrance where the first young born to the colony emerged in 1973. Old entrance 32 was the only one known to have been opened by digging from below the ground to the surface. The tunnel leading from it was the most nearly vertical (estimated 80 degrees). Others entered the ground at a 25- to 40-degree angle.

Even though the samples were small, the burrows of Utah prairie dogs described herein did not differ significantly from those of other whitetailed species. Although *C. leucurus* and relatives are usually regarded as true hibernators, there seem to be no consistent differences between the underground systems of whitetailed and the non-hibernating black-tailed prairie dogs. Some variations in burrow design apparently related to local soil, rock, and gravel strata conditions (Wilcomb 1954) or height of the water table and periodic flooding have been reported (Foster 1924; Whitehead 1927). Utah prairie dogs made no modifications to prevent occasional flooding of their burrows from heavy rains in Washington, D.C.

ACKNOWLEDGMENTS

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LITERATURE CITED

CLARK, T. W. 1977. Ecology and ethology of the white-tailed prairie dog (*Cynomys leucurus*). Milwaukee Pub. Mus. Biol. and Geol. No. 3. 97 pp.

FOSTER, B. E. 1924. Provisions of prairie-dog to escape drowning when town is submerged. J. Mammal. 5:266–268.

LONGHURST, W. 1944. Observations on the ecology of the Gunnison's prairie dog in Colorado. J. Mammal. 25:24–36.

PIZZIMENTI, J. J., AND G. D. COLLIER. 1975. *Cynomys parvidens*. Mammalian Species No. 52. Amer. Soc. of Mammal. 3 pp.

WHITEHEAD, L. C. 1927. Notes on prairie dogs. J. Mammal. 8:58.

WILCOMB, M. J. 1954. A study of prairie dog burrow systems and the ecology of their arthropod inhabitants in central Oklahoma. Unpublished dissertation. Univ. of Oklahoma, Norman.

MULE DEER PASSAGE BENEATH AN OVERLAND COAL CONVEYER

Charles L. Greenwood[1] and Larry B. Dalton[2]

Abstract.— Presently, information pertaining to migration and daily movement patterns of big game in relation to overland conveyors or large diameter pipelines is sparse. A literature review showed that moose (*Alces alces*), caribou (*Rangifer tarandus granti*), reindeer, and dall sheep (*Ovis dalli dalli*) will pass beneath or over large diameter pipeline systems. But no information was found relative to big game crossing coal conveyor systems. Mule deer (*Odocoileus hemionus*) passage beneath an overland coal conveyor in Carbon County, Utah, was studied during spring 1981. Deer avoided crossing at underpass opportunities where the clearance was less than 50 cm. Clearances between 50 and 90 cm were selected for crossing. Deer passed beneath the conveyor during day and nighttime conditions and while the conveyor was either operating or idle. Recommendations are discussed for designing conveyors and pipelines to facilitate big game passage.

Wildlife agencies are presently faced with assessing the impacts of diverse development on wildlife. They are frequently forced to perform such assessments without the benefit of substantial information or guidelines. One area of particular concern to the Utah Division of Wildlife Resources is the creation of barriers to big game migration. This paper will focus on barriers such as overland conveyor systems and large-diameter aboveground pipelines. Typically, without adequate precautions, these structures cannot be crossed by big game animals. Increased industrial use of these structures has prompted the need for understanding the impacts of big game movement. Transportation of water, gases, minerals, and other products over long distances by use of overland conveyors, slurry lines, or large-diameter pipelines is a historic practice. The economic feasibility of such has been enhanced by escalating fuel costs and prospects of using saline water in slurry lines. These structures can create migration as well as daily movement problems for big game.

A review of pertinent literature and surveys of other wildlife agencies in the West indicate that the Trans-Alaska Pipeline is the only similar structure that has been studied relative to big game movement. Child (1973) assessed the reactions of caribou to various aboveground designs of simulated pipelines in Prudhoe Bay, Alaska. Most caribou (78%) approaching the simulation either reversed their direction of movement or circumvented the structure. When crossings were made, overpass ramps were utilized three times more often than underpasses. Avoidance of the Trans-Alaska Pipeline during migration, and abandonment of most calving in the Prudhoe Bay area continue to be a problem (Cameron et al. 1979, Cameron and Whitten 1982). Child and Lent (1973) found the responses of semidomesticated reindeer to be similar to that of caribou.

Van Ballenberghe (1978) evaluated the reaction of moose to the Trans-Alaska Pipeline. Moose rarely moved over pipeline sections that had recently been buried. Most moose crossings were beneath pipeline sections elevated 1.8 m or more. Hinman (1974) noted that moose along the Davidson Ditch Pipeline near Fairbanks, Alaska, would not cross at clearances less than 1.5 m.

Dall sheep in Alaska are known to cross beneath pipelines providing 1.5 m clearance during migration (W. Smith, pers. comm., Alaska Department of Fish and Game).

In an effort to understand the effects of an overland coal conveyor on mule deer migration and daily movements in Utah, a recently constructed conveyor was studied.

Study Site

The overland coal conveyor is in Wattis Canyon, Carbon County, Utah (39°31′ N

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Lat., 111°02′ W Long.), and is operated by Plateau Mining Company's Star Point Mine. Wattis Canyon is on the east side of the Wasatch Plateau, and drains from west to east. The canyon sides are steep and support a mountain brush vegetative type. Scattered stands of Douglas fir (*Pseudotsuga menziesii*) are located in the drainages of the north-facing slope. Predominant vegetation at the mouth of the canyon consists of pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*) interspersed with sagebrush (*Artemisia tridentata* and *A. nova*). The conveyor system is situated near the base of the north-facing slope.

Most deer use of this area occurs during fall and spring migration, although a few deer remain yearlong. Alignment of the conveyor is such that it generally parallels the drainage as well as the direction of spring and fall deer migrations. The conveyor extends downslope 1.4 km from the edge of deer summer range into winter range. The conveyor structure is 1.8 m wide, covered by corrugated metal with vertical leg supports spaced 6.1 m apart. It emits a constant noise while operating that measures 77 decibels (comparable to an idling vehicle) at a distance of 1 m.

METHODS

Between 10 April and 4 May 1981, 9 inspections of Plateau's conveyor were conducted to document evidence of tracks or direct observation of deer crossing beneath the conveyor. The winter and spring of 1981 was comparatively dry, with little snow accumulation. No snow was present during the study period. Two short sections of the conveyor were not monitored: the tipple (discharge) end at the terminus of the conveyor, which provided clearances greater than 3 m; and the portal end, which was positioned next to the ground, thus allowing no clearance. Passage opportunity greater than 3 m was assumed (based on field observation of deer at another conveyor structure) to not interfere with movement.

In addition, 149 random measurements were taken along the monitored length of the conveyor to estimate statistics relative to clearance beneath it. Correlation analysis, chi-square analysis, and Bonferroni normal statistics (Neu et al. 1974) were used to quantitatively analyze the data.

RESULTS AND DISCUSSION

During the study period, 150 mule deer crossings under the conveyor were documented. Surveys to determine the presence of deer migration trails revealed numerous routes adjacent to the conveyor. Most trails paralleled the structure. The few that bisected it were usually obliterated by construction activity. The mean clearance and standard error (SE) beneath the conveyor for observed deer crossings was 70.8 (1.3) cm. Random measurements along the conveyor showed the mean clearance to be 67.8 (3.5) cm. Correlation analysis of clearance categories 30 cm or greater showed a significant correlation between the actual deer crossings and random measurements ($r = 0.81$, $P < 0.001$). This would appear to indicate that the proportion (availability) of the various clearances along the conveyor determined the amount of deer use in each clearance category (Table 1).

However, further evaluation through chi-square analysis (goodness-of-fit test) showed a significant difference between the observed and expected number of deer crossings for the various clearance categories ($\chi^2 = 78.5$, 6 d.f., $P < 0.0005$). Thus the hypothesis that the number of deer crossings within each clearance category was proportional to the availability of each clearance category was rejected. Next, the analysis technique developed by Neu et al. (1974) was used to determine which clearance categories were avoided and which were preferred for crossings. Comparisons of the expected proportion of deer crossings in each clearance category, to the 99% confidence interval on observed proportions of deer crossings, were made. Deer crossed at clearances of 50 to 90 cm significantly more than expected; 88% of the deer crossings were made within this range of clearances, although only 56% of the crossings were expected. Clearances of 90 to 130 cm were used in proportion to their availability; 9% of the deer crossings were observed in this range of clearances, and 7% were expected. The two remaining clearance categories, 0 to 50 cm and 130 to 150 cm, were used significantly less than expected: 3% of the deer crossings were observed, but 32% were expected in the lowest category, and 1% of the deer crossings were observed in the highest category when 5% was expected (Tables 1 and 2).

Undoubtedly, clearances less than 50 cm were avoided. This is partly explained because of the difficulty for most mule deer to physically squeeze beneath structures providing less than 30 cm clearance. However, Falk et al. (1978) have documented white-tailed deer (*Odocoileus virginianus*) to crawl under highway fences where gaps of only 23 cm existed. For the lowest crossing documented beneath the conveyor (33 cm), drag marks and hair were left by the mule deer. Also, during times of conveyor operation it is speculated that the presence of a moving belt, and it possibly rubbing the deer's back, would hinder crossing at such low clearances.

Clearances from 50 to 130 cm were readily used by deer (the range of heights from 50 to 90 cm appeared to be preferred), but clearances greater than 130 cm seemed to be avoided. It is our opinion that once suitable clearance was provided (50 cm) and all other circumstances were acceptable, a crossing was made. The apparent preference by deer for heights ranging from 50 to 90 cm is most likely explained by the high availability (56%) of crossing opportunities along the conveyor in this category. What seems to be avoidance, from a statistical perspective, of the 130 cm or greater heights is misleading. It may simply reflect the presence of human activity near those portions of the conveyor (the tipple-loadout area), or the high likelihood that deer would encounter suitable crossing opportunity first (only 5% of the crossing opportunities were of heights greater than 130 cm).

Behavioralobservationsof22deer-conveyor interactions were made. No deer attempted to jump over the structure. Deer passed beneath the conveyor at times when it was in operation as well as when it was idle. Deer did pass during both day and night conditions. Some deer showed signs of anxiety when near the conveyor, but others gave no indication of concern. A few deer refused to cross even though highly motivated and sought alternate routes.

In Alaska, Child (1973) reported that small groups of caribou were more apt to cross the simulated pipeline than large groups. Adult bulls of mixed herds usually went around the simulated pipeline. Nursery bands or groups under female leadership investigated and made the most use of crossing structures. Crossing of the simulated pipeline often resulted in splitting of herd groups, and in some cases separated cows from calves for up to two hours. Hinman (1974) noted that moose in Alaska always made a crossing, when suitable opportunities were provided, within 800 m of the point where the animal first encountered the pipeline. Use of crossing structures was also highly correlated with the level of insect harassment.

Table 1. Number of mule deer passages and random measurements per clearance category, Plateau Mining Company's overland coal conveyor, Carbon County, Utah, 1981.

Clearance categories (cm)	Number of deer passages	Number of random measurements	Clearance categories (cm)	Number of deer passages	Number of random measurements
0–30	0	21	90–95	2	3
30–35	1	8	95–100	2	3
35–40	0	5	100–105	1	1
40–45	1	4	105–110	5	1
45–50	2	10	110–115	1	0
50–55	9	11	115–120	0	0
55–60	25	12	120–125	1	3
60–65	21	15	125–130	1	0
65–70	23	16	130–135	0	1
70–75	25	17	135–140	0	0
75–80	17	5	140–145	1	0
80–85	5	5	145–150+	0	6
85–90	7	2			

RECOMMENDATIONS

Unfortunately, with the limited amount of information relative to big game passage under or over barriers, much speculation is involved in making recommendations at this time.

When planning and designing an overland conveyor system or similar structure, there are several important considerations. The known or projected response of big game to the structure must be considered. This not only includes big game already present, but also species that could potentially inhabit the area. Thus far, researchers have measured varying responses by big game to barrier structures. Experience from the Trans-Alaska Pipeline and similar barriers indicates that moose will cross under a structure elevated to allow at least 1.5 to 1.8 m of clearance with minimal accumulation of snow (Van Ballenberghe 1977, Hinman 1974). Caribou are much more sensitive and prefer to avoid structures. During times of stress (migration and insect harassment) they sometimes attempted to cross, preferring to use overpasses (Child 1973, Cameron et al. 1979, Cameron and Whitten 1982). No information was found on elk (*Cervus elaphus*), but we suspect that elk response to a barrier structure would be similar to that of caribou.

Site-specific factors must also be considered. Design of crossing structures must take into account snow accumulation and vegetation growth beneath the structure, which could effectively reduce the passage clearance during certain seasons. Topography of the area should be considered in the design. Canyons and washes provide natural locations for underpass opportunities, and cutbanks through hillsides and ridges can be developed into overpass structures.

Overland coal conveyors must have either a sufficient number of strategically placed passage structures to allow big game movement, or be adequately elevated along at least 60% to 70% of the total conveyor. The first option requires site-specific studies relative to big game migration and daily movement patterns.

Construction of underpass opportunities demands the greatest attention to individual species requirements. Mule deer use highway underpasses with varying degrees of success (Reed et al. 1975, Reed 1981, Ward 1978). These highway underpasses were typically 3.05 m wide and 3.05 m high. In central Utah, deer use underpasses along Interstate 15 for both daily movements and migration (Smith and Greenwood 1983). Our study suggests that underpass structures along conveyors require a minimum clearance of 1.0 m for use by mule deer and other species similar in stature, such as pronghorn antelope (*Antilocapra americana*) and bighorn sheep (*Ovis canadensis*). A minimum clearance of 3.0 m is recommended for moose and elk. These recommendations allow for snow accumulation and vegetation growth under the structure. The width for underpass opportunities will most likely be determined by the support structures required to meet engineering specifications, but should be as wide as possible. Vertical support structures are

TABLE 2. Observed and expected frequencies of mule deer crossing under Plateau Mining Company's overland coal conveyor, Carbon County, Utah, 10 April–4 May 1981.

Clearance categories (cm)	Observed		Expected[a]		99% confidence interval on Pi[b]	Selection behavior[c]
	N	Proportion (Pi)	N	Proportion		
0 to 30	0	0.0	21	0.141	—[d]	avoided
30 to 50	4	0.027	27	0.181	0.015–0.069	avoided
50 to 70	78	0.520	54	0.362	0.390–0.650	preferred
70 to 90	54	0.360	29	0.195	0.235–0.485	preferred
90 to 110	10	0.067	8	0.054	0.002–0.132	indifferent
110 to 130	3	0.020	3	0.020	0.016–0.056	indifferent
130 to 150+	1	0.007	7	0.047	0.015–0.029	avoided
Total	150		149			

[a] Derived from random measurements.
[b] From Neu et al. (1974).
[c] Clearances avoided were used significantly less than expected; clearances preferred used significantly more; clearances indifferent used as expected.
[d] No confidence interval on O observation.

located every 18.3 m along the Trans-Alaska Pipeline (Van Ballenburghe 1978). Plateau's coal conveyor provides a width of 6.1 m between support structures. A minimum width of 6 m is recommended for deer and similar big game, and 18 m for moose and elk.

Information relative to an overpass structure is limited. Bridges are sometimes constructed across canals to provide a crossing opportunity for big game; Latham and Verzuh (1971) recommend these bridges to be at least 2.4 m wide with 10 cm of soil on top. Child (1973) constructed ramps over the simulated barrier that were approximately 30 m wide and long with 2:1 or 5:1 (horizontal to vertical) side-slopes fanning out 360 degrees from the barrier. Along the Trans-Alaska Pipeline overpasses are constructed as mounds 9 m wide (W. Smith, pers. comm.).

Based on this information, it is recommended that overpass structures be designed as circular earthen ramps bisected by the conveyor. The round shape should not repel animals that are foraging or moving along the barrier, and would encourage animals approaching from any direction to move up and over the barrier. Each half of the ramp should provide a travel path with side-slopes no greater than 60% from horizontal. The two halves should be connected by a 10-m wide platform spanning the barrier. However, burying a conveyor for a distance of at least 15 m would be a better alternative than constructing overpasses. Buried segments of the Trans-Alaska Pipeline 15 to 25 m in length are most acceptable to caribou (W. Smith, pers. comm.).

Additional planning and design of passage structures should include providing a safe travel-way to move big game up to and beyond barriers. Consideration should be given to development of mature trees and an abundance of browse and grass-forb communities along and approaching the barrier and at crossing opportunities.

In this study on deer, evaluation of behavior was limited. No determination of the number of deer deflected by the conveyor was made. This study simply documents the clearance heights of a barrier under which some deer will pass. Only through continued research on mule deer and other big game will the full impact of such barriers be understood, and additional mitigation techniques developed.

Acknowledgments

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Literature Cited

Child, K. N. 1973. The reactions of barren-ground caribou (*Rangifer tarandus granti*) to simulated pipeline and pipeline crossing structures at Prudhoe Bay, Alaska. Compl. Rep. Alaska Coop. Wildl. Res. Unit, Univ. of Alaska, Fairbanks. 51 pp.

Child, K. N., and P. C. Lent. 1973. The reactions of reindeer to a pipeline simulation at Penny River, Alaska. Interim Rep., Alaska Coop. Wildl. Res. Unit, Univ. of Alaska, Fairbanks. 29 pp.

Cameron, R. D., and K. R. Whitten. 1982. Effects of the Trans-Alaska Pipeline on caribou movements. Alaska Department of Fish and Game. Fed. Aid Wildl. Rest. Proj. W-21-1 and W-21-2, Job No. 3.18R. 25 pp.

Cameron, R. D., K. R. Whitten, W. T. Smith, and D. D. Roby. 1979. Caribou distribution and group composition associated with construction of the Trans-Alaska Pipeline. Can. Field-Natur. 93:155–162.

Falk, N. W., H. B. Graves, and E. D. Bellis. 1978. Highway right-of-way fences as deer deterrents. J. Wildl. Manage. 42:646–650.

Hinman, R. 1974. The impact of oil development on wildlife populations in northern Alaska. Pages 156–164 *in* Proc. 54th Ann. Conf. of West. Assoc. State Game and Fish Comm. Albuquerque, New Mexico.

Latham, H. S., and J. M. Verzuh. 1971. Reducing hazards to people and animals of reclamation canals. U.S. Bur. Reclamation Rep. No. REC-ERC-71-36. 30 pp.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38:541–545.

Reed, D. F., T. N. Woodard, and T. M. Pojar. 1975. Behavioral response of mule deer to a highway underpass. J. Wildl. Manage. 39:361–367.

Reed, D. F. 1981. Mule deer behavior at a highway underpass exit. J. Wildl. Manage. 45:542–543.

Smith, R. B., and C. L. Greenwood. 1983. Big game use along the proposed Mona-Nephi-Sevier Canal alignments, irrigation and drainage system, Bonneville Unit, Central Utah Project. Utah Div. Wildl. Resour. prep. for U.S. Dep. Inter. Bur. of Reclamation. 82 pp.

VAN BALLENBERGHE, V. 1978. Final report on the effects of the Trans-Alaska Pipeline on moose movements. Joint State/Fed. Fish and Wildl. Adv. Team, Spec. Rep. No. 23, Anchorage. 41 pp.

WARD, A. L. 1978. The effects of highway operation practices and facilities on elk, mule deer, and pronghorn antelope. Ann. Rept., Proj. No. 942-41-42-13-0088-33F2-6-2580, cont. Fed. Highway Adm. Rep. No. FHWA-RD-76-174.

CRANIAL MEASUREMENTS OF THE COLUMBIAN GROUND SQUIRREL (*SPERMOPHILUS COLUMBIANUS COLUMBIANUS*), WITH SPECIAL REFERENCE TO SUBSPECIES TAXONOMY AND JUVENILE SKULL DEVELOPMENT

Charles L. Elliott[1] and Jerran T. Flinders[2]

Abstract.— The Columbian ground squirrel (*Spermophilus columbianus* (Ord)) is represented by two recognized subspecies, *S. c. columbianus* (Ord) and *S. c. ruficaudus* (A. H. Howell), that occupy allopatric but adjacent geographical areas in Washington, Oregon, and Idaho. Since numerical cranial characteristics of these subspecies have not been documented, we measured 8 cranial characteristics on 94 adult and 32 juvenile Columbian ground squirrels in an area considered to be occupied by *S. c. columbianus*. Body weights and standard body measurements were recorded for adults and juveniles. The study area included portions of the River of No Return Wilderness Area in central Idaho. Howell's (1938) original descriptions seemed to differentiate *S. c. ruficaudus* from our sample of Columbian ground squirrels. Juvenile Columbian ground squirrels did not attain full cranial development until their second season. Length of maxillary tooth row in juveniles, especially females, may closely approximate adult dimensions by the end of their first summer.

There are 11 Holarctic species recognized in the subgenus *Spermophilus* Cuvier and 8 of these occur in North America (Hall 1981:382, Nowak and Paradiso 1983:501). One member of this group is the Columbian ground squirrel (*Spermophilus columbianus* (Ord)), a sciurid endemic to the Pacific Northwest (Fig. 1). Howell (1938) examined specimens of Columbian ground squirrels and separated the species into two subspecies of *S. c. columbianus* (Ord) and *S. c. ruficaudus* (A. H. Howell). The two subspecies are differentiated as follows: (1) coat color: *ruficaudus* is tawny (not gray) on the upper side of the tail, sides of its face and throat are a deeper shade of tawny and its legs and feet are darker; (2) external anatomy: *ruficaudus* have larger hind feet; and (3) cranial characteristics: the skull of *ruficaudus* is larger and relatively broader than *columbianus*, the jugal wider and zygomata more heavily built (Howell 1938).

The cranial dimensions of either subspecies of the Columbian ground squirrel have not been examined. As a result of recent field studies (Elliott and Flinders 1980a,b), we obtained skulls from a large number of adult and juvenile Columbian ground squirrels. The purpose of this note is to report how the measurements obtained from these specimens compare to Howell's criteria for subspeciation and to note the extent of cranial development exhibited by juvenile ground squirrels at the end of their first season of activity.

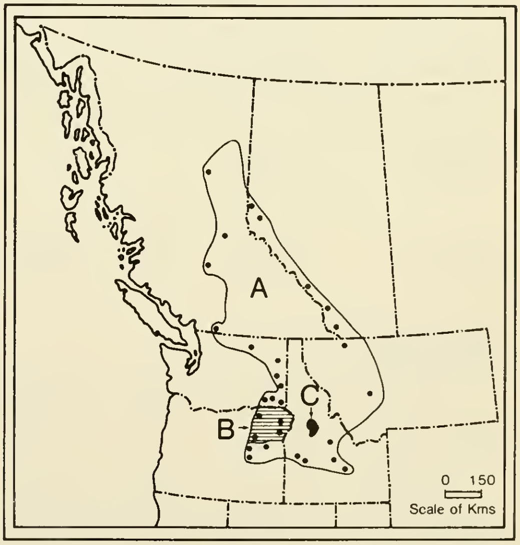

Fig. 1. Range of *Spermophilus columbianus* in North America. Area A represents the range of *S. c. columbianus*; area B represents the range of *S. c. ruficaudus*, and area C indicates location of the Idaho Primitive Area. Black circles correspond to specimen locations used by Hall (1981:389) in establishing subspecies boundaries.

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STUDY AREA AND METHODS

Ground squirrels were collected from four sites within the Big Creek drainage of the Idaho Primitive Area (IPA) (now called the River of No Return Wilderness Area). Physiography and vegetation of the Big Creek area have been described by Hornocker (1970). The Cold Meadows study site (elev. 2142 m) typified the mountain meadow habitat type utilized by Columbian ground squirrels in the IPA. Rush Point (elev. 1890 m) represented the *Artemisia tridentata*-bunchgrass association typical of the southeast-facing slopes occupied by *S. columbianus*. The Big Creek (elev. 1750 m) and Cabin Creek (1067 m) squirrel colonies were located in unused horse pastures, areas representative of the many abandoned homesteads and ranches found throughout the IPA.

Physical measurements and skull samples were obtained from squirrels live-trapped and shot. Skulls were skinned, dried, and placed in a dermestid beetle (*Dermestes maculatus*) colony for cleaning. Only squirrels meeting the following minimal weight criteria were used in this study: June body weight—400 g, July—500 g, and August—600 g. These categories were used in an attempt to eliminate yearling squirrels from calculations. Mark-recapture data at the Cold Meadows and Rush Point sites indicated one-year-old squirrels emerging from hibernation exhibited early season body weights of approximately 300 g (unpublished data). Michener (1977) also separated age classes of Columbian ground squirrels based on weight, finding that females weighing over 400 g and under 300 g could reliably be classed as adults and yearlings, respectively. It was therefore concluded that use of the aforementioned weight categories (400, 500, 600 g) assured that only adult Columbian ground squirrels would be included in the calculations. Ground squirrels referred to as juveniles in this study are squirrels in their first summer of life (= young of the year). Eight skull parameters (defined in Hall 1981:133–137) were measured (see Table 1). All measurements were taken to the nearest 0.1 mm with dial calipers.

RESULTS AND DISCUSSION

Ninety-four adults and 32 juvenile Columbian ground squirrel skulls of the subspecies

TABLE 1. Cranial measurements (mean ± S.D.) of adult Columbian ground squirrels from four sites in the Idaho Primitive Area and Howell's (1938) data. Sample size in parentheses. Idaho data are for *Spermophilus columbianus columbianus*.

Location	Diastema	Occipito-nasal length	Palatilar length	Zygomatic breadth	Mastodial breadth	Inter-orbital breadth	Nasal length	Maxillary tooth row length
				(Measurements in mm)				
IDAHO PRIMITIVE AREA								
Cold Meadows								
Males (23)	11.8±0.7	51.3±1.9	25.4±0.9	32.2±1.7	25.7±0.9	10.9±0.7	18.2±0.9	11.7±0.4
Females (23)	11.6±0.6	50.4±0.9	25.2±0.6	32.0±0.8	25.1±0.6	10.7±0.7	18.2±1.2	11.5±0.5
Rush Point								
Males (17)	11.7±0.8	51.1±1.9	25.6±0.9	32.6±1.5	25.9±1.4	10.9±0.6	17.3±2.6	11.5±0.4
Females (13)	11.2±0.9	49.3±1.9	24.5±0.8	30.7±2.0	24.9±1.5	10.6±0.7	17.7±1.4	11.6±0.5
Big Creek								
Males (8)	9.9±0.6	46.9±1.5	24.3±0.7	28.9±1.8	23.4±0.6	9.9±0.4	16.1±1.1	11.6±0.5
Cabin Creek								
Males (6)	11.1±0.4	50.0±1.3	25.1±0.8	30.7±0.6	24.4±0.7	10.1±0.4	17.5±0.5	11.8±0.4
Females (4)	11.5±0.8	49.2±1.1	24.8±0.3	31.3±0.7	25.7±2.7	10.5±0.6	17.7±0.8	11.3±0.9
HOWELL'S 1938 DATA								
S. c. columbianus								
Males (10)	*	51.7	25.1	31.8	*	10.6	19.4	10.9
Females (7)	*	50.7	24.8	32.2	*	11.2	18.7	11.1
S. c. ruficaudus								
Males (8)	*	54.2	26.6	34.1	*	12.4	19.8	11.4
Females (4)	*	52.9	25.7	33.3	*	12.5	19.3	11.3

TABLE 2. Cranial measurements (mean ± S.D.) of juvenile Columbian ground squirrels from three sites in the Idaho Primitive Area. Sample size in parentheses. Data for *Spermophilus columbianus columbianus.*

	Sites				
	Cold Meadows		Rush Point		Cabin Creek
Measurement	Males (6)	Females (6)	Males (11)	Females (5)	Females (4)
Diastema	10.8 ± 0.6mm	10.6 ± 0.8	10.3 ± 0.6	9.9 ± 0.6	10.6 ± 0.4
Occipotonasal length	47.4 ± 1.1	46.3 ± 2.0	47.4 ± 2.6	44.9 ± 1.9	47.3 ± 2.2
Palatilar length	23.7 ± 0.5	22.9 ± 1.2	23.9 ± 1.2	21.6 ± 1.6	24.9 ± 0.4
Zygomatic breadth	28.5 ± 1.2	28.9 ± 2.4	27.8 ± 0.7	27.7 ± 0.9	29.1 ± 1.1
Mastodial breadth	23.9 ± 0.6	23.3 ± 1.7	23.1 ± 0.7	22.2 ± 1.1	24.2 ± 0.7
Interorbital breadth	9.8 ± 0.2	9.8 ± 0.5	9.6 ± 0.4	9.5 ± 0.5	9.5 ± 0.6
Length of nasals	16.2 ± 0.9	16.2 ± 0.9	15.7 ± 0.7	15.2 ± 1.3	16.4 ± 1.3
Maxillary tooth row	11.7 ± 0.3	11.6 ± 0.8	11.4 ± 0.5	11.2 ± 0.5	11.6 ± 0.5

S. c. columbianus were measured (Tables 1 and 2). No statistical comparison between our skull measurements and Howell's (1938) data are possible (Howell lists only the category mean and range of values), but certain trends are evident. The mean interorbital breadth, length of nasals, and greatest skull length (occipitonasal length) given by Howell for *ruficaudus* are larger than corresponding values obtained for *columbianus* (Table 1). This would tend to support Howell's subspeciation criteria that *ruficaudus* skulls are larger and broader than *columbianus.* Howell also noted that *ruficaudus* had larger hind

TABLE 3. Mean (± S.D.) total body length, hind foot length, and ear length (mm) of adult Columbian ground squirrels from four sites in the Idaho Primitive Area, two museum collections, and Howell's (1938) data. Sample size in parentheses.

Location	Total body length	Hind foot length	Ear length
IDAHO PRIMITIVE AREA[1]			
Cold Meadows			
Male (64)	334.9 ± 14.2	50.5 ± 1.7	19.7 ± 1.3
Female (72)	326.3 ± 12.4	49.0 ± 1.9	19.2 ± 1.1
Rush Point			
Male (34)	328.2 ± 16.5	49.4 ± 1.8	19.4 ± 1.4
Female (41)	327.5 ± 14.1	46.7 ± 2.1	19.0 ± 1.0
Big Creek			
Male (11)	333.8 ± 16.5	51.4 ± 1.9	19.5 ± 0.7
Female (3)	325.0 ± 15.0	51.3 ± 1.5	19.7 ± 0.6
Cabin Creek			
Male (3)	341.7 ± 7.6	51.3 ± 2.3	19.7 ± 1.2
Female (5)	328.6 ± 10.6	49.6 ± 0.9	20.0 ± 0.7
UNIVERSITY OF IDAHO MUSEUM[1]			
Male (10)	337.6 ± 13.5	49.7 ± 2.0	22.5 ± 3.5
Female (11)	337.3 ± 17.3	48.7 ± 2.0	23.0 ± 2.7
UNIVERSITY OF MONTANA ZOOLOGICAL MUSEUM[1]			
Male (7)	366.1 ± 18.8	52.1 ± 3.7	17.8 ± 2.9
Female (9)	348.4 ± 23.0	47.9 ± 2.9	15.9 ± 3.3
HOWELL'S 1938 DATA			
Spermophilus columbianus columbianus			
Male and female (12)	349.7 (327–377)[2]	51.2 (48–55)	–
Spermophilus columbianus ruficaudus			
Male and female (10)	369.6 (340–410)	54.2 (51–58)	

[1] Data for *Spermophilus columbianus columbianus.*

[2] Range of values given by Howell (1938).

TABLE 4. Skull size of juvenile Columbian ground squirrels expressed as a percent of average skull dimensions of adults taken during the same collection period, August 1977–1978, Idaho Primitive Area.

	Sites				
	Cold Meadows		Rush Point		Cabin Creek
Measurement	Males	Females	Males	Females	Females
Diastema	92	91	88	89	92
Occipitonasal length	92	92	93	91	96
Palatilar length	93	91	94	88	100
Zygomatic breadth	89	90	85	90	93
Mastodial breadth	93	95	89	89	94
Interorbital breadth	90	92	88	90	90
Length of nasals	89	89	91	86	93
Maxillary tooth row	99	100	99	97	100

feet than *columbianus* (Table 3). This characteristic of subspeciation also appears to be valid. Howell's *ruficaudus* hind foot length and associated range of values exceed all values found in Idaho and other locations occupied by *columbianus* (Table 3). Based on data reported here and by Howell (1938), an additional parameter for justifying *ruficaudus* as a valid subspecies is total body length. *Spermophilus c. ruficaudus* appears to be a longer squirrel than *columbianus*, exceeding all reported *columbianus* values for total body length (Table 3).

Juvenile ground squirrels often exhibit a delay in attaining maturity (Bridgwater 1966, Morton and Tung 1970). Juvenile Columbian ground squirrels on the Cold Meadows study site do not attain adult size until their second season (Elliott and Flinders 1980b). This same delay in attainment of adult dimensions is also exhibited in cranial development (Table 4). Of the skull parameters measured, the maxillary tooth row was the closest to adult size at the end of the first summer. Skull length (occipitonasal length) was approximately 92% of adult size and the skull width (zygomatic breadth) was almost 90% (Table 4).

Based on information available in the literature and data reported here, Howell's (1938) criteria used in establishing two subspecies within *Spermophilus columbianus* are valid. Additional data concerning the physical and cranial dimensions of *Spermophilus columbianus ruficaudus* are needed to further establish the validity of the two subspecies.

We thank the University of Idaho for permission to use the facilities at the Taylor Ranch Field Station, Idaho Primitive Area.

LITERATURE CITED

BRIDGWATER, D. D. 1966. Laboratory breeding, early growth, development and behavior of *Citellus tridecemlineatus* (Rodentia). Southwestern Nat. 11:325–337.

ELLIOTT, C. L., AND J. T. FLINDERS. 1980a. Seasonal activity pattern of Columbian ground squirrels in the Idaho Primitive Area. Great Basin Nat. 40:175–177.

______. 1980b. Postemergence development and interyear residence of juvenile Columbian ground squirrels in the Idaho Primitive Area. Great Basin Nat. 40:362–364.

HALL, E. R. 1981. The mammals of North America. John Wiley and Sons, New York. 1181 pp.

HORNOCKER, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monograph 21. 39 pp.

HOWELL, A. H. 1938. Revision of the North American ground squirrels. North Amer. Fauna 56:85–90.

MICHENER, G. R. 1977. Effect of climatic conditions on the annual activity and hibernation cycle of Richardson's ground squirrels and Columbian ground squirrels. Canadian J. Zool. 55:693–703.

MORTON, M. L., AND H-C. L. TUNG. 1970. Growth and development in the Belding ground squirrel (*Spermophilus beldingi beldingi*). J. Mammal. 52:611–616.

NOWAK, R. M., AND J. L. PARADISO. 1983. Walker's mammals of the world. 4th ed., Vol. I. Johns Hopkins Univ. Press, Baltimore, Maryland. 568 pp.

LITTORAL HETEROGENEITY AND DIEL BEHAVIOR OF WHITE BASS (*MORONE CHRYSOPS*) AND CARP (*CYPRINUS CARPIO*) IN UTAH LAKE, UTAH

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Abstract.— Diel activity and association patterns of white bass (*Morone chrysops*) and carp (*Cyprinus carpio*) in Utah Lake, Utah, were studied over four 24-hr periods during August 1980. Fish were concurrently sampled from two adjacent littoral habitats. Significant differences existed in diel activity patterns in two of three size classes of white bass and in diel association patterns of white bass and carp between the two habitat areas. Differences in habitat structure, and in biological activity between the habitat types, are implicated as the primary determinants of overall diel activity of fish in these littoral areas.

The temporal structure of fish communities, particularly diel patterns, has received less attention than other structural components such as trophic and spatial patterns (Helfman 1978). Studies of diel distribution patterns and fish behavior have generally examined differences between macrohabitat categories (e.g., littoral and limnetic zones) within lakes (Baumann and Kitchell 1974, Bohl 1980, Carlander and Cleary 1949, Keast and Welsh 1968). Few studies consider differences between adjacent littoral habitat patches, yet field and theoretical ecology continue to demonstrate the role of habitat heterogeneity in structuring populations and communities.

Differences should exist between the diel behavior of fish and habitat heterogeneity. Differences in resource availability between habitats (Ivlev 1961) and concurrent differences in fish association patterns (Larkin 1956, Werner and Hall 1977) suggest that energetic benefits from given strategies of diel behavior are not equal in all habitats. One strategy may yield high net returns of energy in one habitat, but in another net energy returns may be low with the same strategy. No studies specifically treat these ideas with respect to diel behavior, but the general topic of fish-habitat energetics has been examined by others (Glass 1971, Werner and Hall 1974, 1979, Werner, Mittelbach, and Hall 1981).

Two studies suggest the existence of within-habitat differences in fish diel activity. Helfman (1979a) noted within-population variation in diel activity patterns of yellow perch (*Perca flavescens*). He suggested that they may be due to genetic variation, fixed patterns of response to environmental conditions that differ between areas, or overall generalist adaptation of fish to historically varying environmental factors. These environmental factors included photic condition, predation pressure, food availability, water clarity, twilight length, and lake size. Hall et al. (1979) noted that a variable fraction of a golden shiner (*Notemigonus crysoleucas*) population underwent offshore diel migrations on different dates, and no diel separation occurred in their feeding on littoral and planktonic prey.

Our study examines several questions raised by these two investigations. Specifically, we focused on whether or not the same fish species, and size classes within those species, exhibited significantly different patterns of diel activity and association between different but adjacent littoral habitats. Differential patterns of diel activity and association may indicate adaptive behavior of fish in response to a locally heterogeneous environment.

Study Site and Methods

This study was conducted on Utah Lake (Fig. 1), a large, shallow lake in north central

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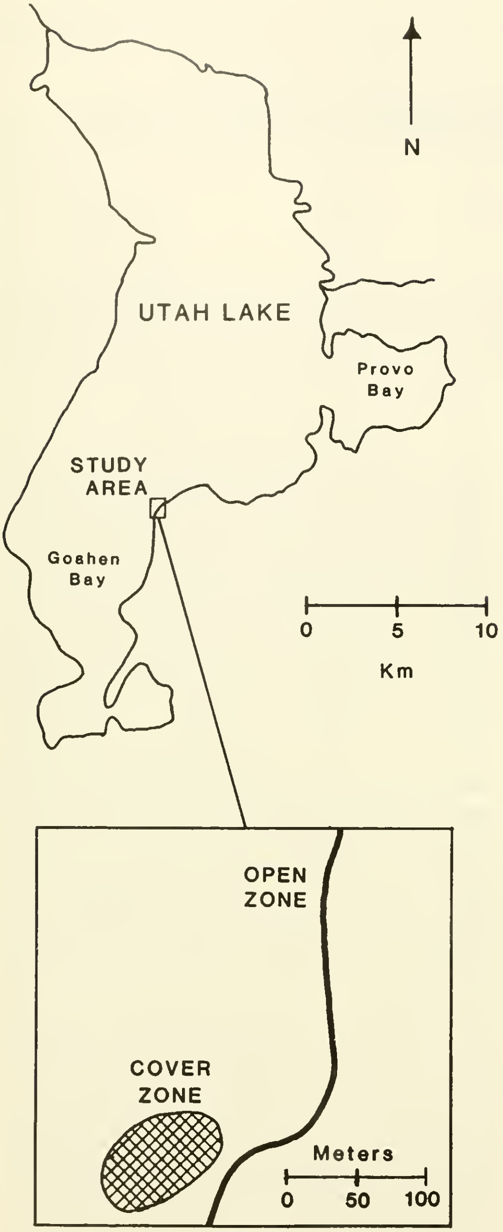

Fig. 1. Utah Lake (top) and the study site at Goshen Bay (bottom), showing the two habitat areas.

Utah approximately 25 km south of Salt Lake City. The lake has a surface area of approximately 38,000 ha, a mean depth of 2.9 m, and a maximum depth of 4.2 m. Utah Lake is described as being eutrophic, turbid, and slightly saline (Fuhriman et al. 1974). The water exhibits a high sulfate and carbonate content (Shiozawa 1975), and marl is being actively deposited in several shoreline areas. Conductivity levels range between 500 and 1700 micromhos (mean 1200). Secchi disk readings are between 12 and 50 cm (mean 24 cm) (Shiozawa and Barnes 1977). Water temperatures range from 0 C in winter to 30 C in summer, with temperatures decreasing rapidly in the late fall and increasing rapidly in spring. Utah Lake is usually covered with 10–15 cm of ice from mid-December to mid-February (Tillman and Barnes 1973). During ice-free months it is polymictic, and no thermal stratification occurs.

Most of Utah Lake has a mud-ooze substrate, but many littoral areas contain sand, gravel, rubble, clay, and hardpan. Rooted aquatic vegetation is sparse, and algal blooms occur in various areas of the lake, especially during late summer.

During August 1980 (August 4–5, 11–12, 18–19 and 21), fish were sampled over 24-hr periods from two adjacent habitat patches within the rubble-littoral zone along the eastern shore of Goshen Bay. Two trap nets with 15-m leads were concurrently placed within each habitat zone, and fish were removed at 4-hr intervals. Specimens from each pair of nets were then pooled and classified to species and length.

Open and Cover Zones

The open habitat zone (Fig. 1, bottom inset), comprised a 50-m stretch of shoreline containing a large rubble–small boulder substrate with a sand-gravel matrix. This area was devoid of rooted macrophytes and had a mean depth of 1 m and a maximum depth of 1.8 m. Beyond this depth the substrate was a mud ooze. The other habitat, the cover zone, was located 200 m south. It encompassed a stretch of shoreline containing thick reed growth separated at intervals by narrow channels. The substrate was a large rubble–small boulder composition, but it also contained a thick matrix of silt and mud. The mean depth within this habitat zone was .95 m, the maximum 1 m. Between these two areas there was a gradient of reed cover. Water temperature (at one-half maximum depth) during the study was 26.5 C in the open zone and 23.5 C in the cover zone. The conductivity level in both habitats was 1450 micromhos.

Trap nets were placed with leads and trap openings towards shore. In the open zone leads extended to shore due to the steep gradient. In the cover zone, nets were placed in channels between reed beds, but because of a more gradual slope the leads did not extend to shore.

Results and Discussion

We assume that the differences in the proportion of fish caught between time intervals corresponded to differences in activity levels of the fish (Carlander and Cleary 1949, Lawler 1969, Scott 1955). Some fish species may detect or avoid a net more readily than others (Lawler 1969), and the rate at which nonmigratory fish are caught reveals their entire activity pattern, but the capture of migratory fish reveals only the intensity of their activity while in that area (Carlander and Cleary 1949, Scott 1955). The probability of capture of any given fish species may change with habitat, even if their activity remains constant. For instance, fish feeding in the open zone may utilize a foraging behavior different from that used in the cover zone (Ivlev 1961, Eggers 1977). This influences their probability of capture, and catch rates in each habitat may relate not only to fish activity, presence, and avoidance, but also to the pattern and speed of fish movement (perhaps a function of habitat structure). The use of proportions minimizes but does not eliminate this problem by emphasizing diel changes in percentages rather than numbers.

White bass (*Morone chrysops*) represented 70.5% and carp (*Cyprinus carpio*) 24.9% of the total catch. By habitat, white bass accounted for 72.4% of all fish in the open zone, and carp accounted for 24.4%. In the cover zone, white bass composed 66.4%, and carp made up 25.6%.

Three discrete size classes of white bass were considered. Size I white bass (young-of-the-year < 105 mm) composed 60.5% of that species. Size II white bass (juveniles and subadults, 105–205 mm) accounted for 16.1%, and size III white bass (adults, > 205 mm) represented 23.4% of the catch. Carp showed two discrete groupings. Size I carp (young-of-the-year, ≤ 160 mm) made up 15.4% of that species and size II carp (juveniles through adults, > 160 mm) represented 84.6%. Only 7 carp between 161 and 349 mm were collected.

Walleye (*Stizostedion vitreum*), largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), yellow perch (*Perca flavescens*), black bullhead (*Ictalurus melas*), and Utah sucker (*Catostomus ardens*) were also caught, but collectively accounted for less than 5% of the total.

The fish communities in both the cover and open zones did undergo diel changes in activity. Comparisons within a designated fish size class for between-habitat activity will be termed diel activity patterns. Comparisons between different fish size classes or species will be termed diel association patterns. Differences in diel activity patterns of fish between habitat patches were tested using the Komolgorov-Smirnov, two-sample general distribution test for discretely ordered data. In such application the results are conservative (Gibbons 1976).

Total carp, size I carp, size II carp, total white bass, and size III white bass had no significant differences in activity patterns between open and cover zones (Table 1). However, size I and size II white bass had significantly different patterns of diel activity between the open and cover zones (p = .01 and p = .025, respectively). Open zone size I white bass activity increased from early morning (0600 hr) to midafternoon, but in the cover zone activity began later in the morning (1000 hr) and then rose to the midafternoon peak. Size II white bass peaked in activity in the late afternoon (1800 hr) in the

Table 1. Results of tests for between habitat differences in activity patterns of white bass and carp.

	Open zone vs. Cover zone Level of significance (p-value)
White bass	
All sizes	NS
Size I	.010
Size II	.025
Size III	NS
Carp	
All sizes	NS
Size I	NS
Size II	NS

NS = nonsignificant.

open zone but in the cover zone activity levels peaked in the morning (0600 hr).

Patterns of diel association between fish classes were tested with Spearman's coefficient of rank correlation. Total white bass vs. total carp had no significant diel association patterns in either the open or cover zones. White bass sizes II and III were significantly negatively associated with carp ($.029 < p < .051$, Table 2) in the cover zone.

Variation between sampling days for both activity and association patterns was examined using loglinear models in categorical data analysis. No significant day to day variation in diel activity patterns existed for total white bass or total carp. Significant day-to-day variation occurred in the size I, II, and III white bass. In particular, day 3 was significantly different ($p = .012$) than the other days of the study. This difference occurred between late morning (1000 hr) and early afternoon (1400 hr). Day 3 (August 18) was the only stormy day sampled. The storm represented distinctly different environmental conditions and likely was the cause for the difference in activity patterns observed. Loglinear analysis of day-to-day variation in association patterns between white bass and carp also indicated that day 3 was significantly different within the cover zone ($p = .011$), with more size II and size III being present.

Between-habitat differences in diel activity of size I and II white bass and in diel association of white bass with carp may be caused by the following factors: (1) lateral migration (Emery 1973, Keast 1978, and Nursall 1973), (2) offshore migration (Baumann and Kitchell 1974, Hasler and Bardach 1949, Scott 1955), (3) differential foraging behavior (Pyke, Pulliman, and Charnov 1977, Vinyard 1980, Werner and Hall 1976, Werner and Hall 1979), (4) differential patterns of intraspecific temporal resource partitioning (Hobson 1968, Scott and Crossman 1973), and (5) differential patterns of interspecific temporal resource partitioning (Collette and Talbot 1972, Helfman 1978, Helfman 1979b).

Table 2. Results of tests for diel association between white bass and carp.

	Correlation coefficient 4 Day Totals
Open zone	
All sizes white bass vs. carp	0.100
Size II and III white bass vs. carp	0.214
Cover zone	
All sizes white bass vs. carp	−0.085
Size II and III white bass vs. carp	−0.786*

* = significant at $.029 < p < .051$

Lateral Migration

Higher frequencies of size I white bass were caught in both habitat zones at 1400 hr on day 3 of sampling (August 18–19). Activity levels for size I white bass in the open zone reach a peak earlier in the day (1000 hr vs 1400 hr) and those in the cover zone later (1800 hr vs 1400 hr), when day 3 is removed from the analysis. Size I white bass in the open zone decrease in activity in the afternoon (1400 hr to 1800 hr); concurrently they significantly increase their activity in the cover zone. In the littoral of Goshen Bay, lateral migration of size I white bass into the cover zone at night would by reinforced by the diel activity patterns of their dominant predator, the walleye (see Helfmann 1979a, Werner et al. 1977, viz., predation and the use of refugia by small fish). Walleye were only collected in the open zone and only at night and early morning, with the majority being captured after dark.

Rank correlation between adult walleye and size I white bass in the open zone showed a significant negative association by time ($r^2 = .017$, $p = .029$). Size I white bass have high activity levels during the day within the open zone, but are absent or inactive in that zone at night, the time when walleye are present. Utah Lake walleye also feed on young-of-the-year (size I) carp (Arnold 1960, Dabb and Thompson 1976). Size I carp, like white bass, decrease in activity at night within the open zone as their activity increases within the cover. Rank correlation between walleye and size I carp within the open zone showed no significant diel association, but this is largely due to a midday activity decrease for the carp.

Lateral migration may also occur for size II white bass, but the pattern is not conclusive. Size II white bass increase activity in the open zone later in the morning and cease activity later in the evening than the size I white bass. Size II white bass lengths were usually over 140 mm, and Utah Lake walleye seldom select white bass exceeding 120 mm in length. This size refuge eliminates predation constraints imposed on the predation-susceptible size I white bass.

Offshore Migration

Hall et al. (1979) noted that young-of-the-year golden shiners (*Notemigonus crysoleucas*) did not participate in the evening offshore migration for that species; however, Kelso and Ward (1973) showed that yellow perch fry (*Perca flavescens*) did migrate offshore during the day. The gear types and net mesh used in this study prevented us from making quantitative determinations of offshore movements for size I white bass (also see Hasler and Bardach 1949, Scott 1955, concerning sampling gear inefficiency on small fish); but, based on the trap net data, a complete offshore migration is not likely since size I fish numbers do not drop to zero in either zone.

Size II white bass undergo both lateral and offshore movements. Gill nets set perpendicular to shore (to detect lateral movement) were only slightly lower in catch-per-unit effort compared to gill nets set parallel to shore (to detect offshore movement).

Differential Foraging Behavior

Zooplankton were dominant prey items for size I white bass from both open and cover zones (Devine, unpublished data; see also Dabb and Thompson 1976, Trapnell 1969). Zooplankton densities were approximately equal in both habitat zones (Devine, unpublished data). Thus, if a feeding advantage exists in one habitat zone, it should relate to factors other than food density. If size I white bass are more successful in foraging within the open zone, a morning migration from the cover to the open zone could optimize their food intake (Baumann and Kitchell 1974).

Intraspecific Resource Partitioning

Partial correlation coefficients between white bass size classes were lower in the cover zone than the open zone. Cover zone size II white bass dominated in activity in the early morning, and size I white bass dominated during the afternoon and early evening. Size III white bass were most active during late night and predawn hours. In the open zone a single size class seldom dominated activity. These differences may relate to the habitat structure of the two zones. The open zone, with an absence of reed beds, a steeper slope, and a greater average depth, provided more activity volume per unit of surface area than the cover zone. The compressed activity space within the cover zone may necessitate temporal partitioning of resources by the three size classes of white bass (see Werner and Hall 1977, viz., competition and activity space).

Interspecific Resource Partitioning

Size II and III white bass and carp exhibited no association by time in the open zone, but were significantly negatively associated within the cover zone. Carp had no significant difference in diel activity between the two zones. The white bass size II and III activity differences may relate to the avoidance of carp. Adult carp are primarily benthic feeders (Miller et al. 1959), although they do surface feed (McCrimmon 1968). White bass are primarily planktonic feeders (McNaught and Hasler 1971, Olmstead and Kilambi 1971), but may forage on benthic resources (Dabb and Thompson 1976, Trapnell 1969). Carp are aggressive feeders (Miller et al. 1959), and are much larger than the white bass.

In the cover zone less activity volume was available. White bass and carp, thus brought into closer proximity, would interact more intensely. If competition occurred for space, white bass are at a disadvantage due to their smaller size. Other studies document interference between fish (Janssen 1974, Werner and Hall 1977), but none mention an unintentional effect due to size and feeding behavior. White bass, if displaced by carp in the cover zone, could adjust their behavior through a number of mechanisms, including migration or movement out of the channels. Size I fish had an evening overlap, with carp in the cover zone, but the danger of walleye predation in the open zone at this time may override the disadvantage of interacting with carp (see Werner et al. 1977). Spatial segregation of white bass and carp could more easily occur in the open zone because of the greater depth.

CONCLUSIONS

The patterns of diel activity and association of dominant fish species and size classes in this littoral community were different between habitat zones. Predation forced small fish into cover for protection during the night when the main predator, the walleye, was most active. Different foraging efficiencies between cover and open zones may act to draw these fish from the cover zone into the open zone during the day. Fish that were too large for predators interacted on the basis of inference competition. Carp with their disruptive foraging behavior could displace white bass in the cover zone because of the restricted space (due to reeds and shallowness). The open zone was deeper and lacked the narrow horizontal dimensions of the cover zone. It allowed spatial segregation of carp and white bass, and therefore no interference displacement occurs.

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LITERATURE CITED

ARNOLD, B. B. 1960. Life history notes on the walleye *Stizostedion vitreum vitreum* (Mitchill) in a turbid water, Utah Lake, Utah. Unpublished thesis. Federal Aid Project F-4-R-5, Job T. Salt Lake City, Utah: Department of Fish and Game. 107 pp.

BAUMANN, P. C., AND J. F. KITCHELL. 1974. Diel patterns of distribution and feeding of bluegill (*Lepomis macrochirus*) in Lake Wingra, Wisconsin. Trans. Amer. Fish. Soc. 103:255–260.

BOHL, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. Oecologia 44:368–375.

CARLANDER, K. D., AND R. E. CLEARY. 1949. The daily activity patterns of some freshwater fishes. Amer. Midl. Nat. 41:447–452.

COLLETTE, B. B., AND F. H. TALBOT. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. Los Angeles Co. Nat. Hist. Mus. Sci. Bull. 14:98–124.

DABB, D., AND C. W. THOMPSON. 1976. Food habits of black bullhead, channel catfish, walleye and white bass in Utah Lake, 1975. Utah: Division of Wildlife Resources. 29 pp.

EGGERS, D. M. 1977. The nature of food selection by planktivorous fish. Ecology 85:46–59.

EMERY, A. R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. J. Fish. Res. Board Can. 30:761–774.

FUHRIMAN, D. K., L. B. MERRITT, A. W. MILLER, AND H. S. STOCK. 1974. Hydrology and water quality of Utah Lake. Brigham Young Univ., Provo, Utah.

GIBBONS, J. D. 1976. Nonparametric methods for quantitative analysis. Holt, Rinehart and Winston, New York. 463 pp.

HALL, D. J., E. E. WERNER, J. F. GILLIAM, G. G. MITTELBACH, D. HOWARD, C. G. DONER, J. A. DICKERMAN, AND A. J. STEWART. 1979. Diel foraging behavior and prey selection in the golden shiner (*Notemigonus crysoleucas*). J. Fish. Res. Board Can. 36:1029–1039.

HASLER, A. D., AND J. E. BARDACH. 1949. Daily migrations of perch in Lake Mendota, Wisconsin. J. Wildl. Manage. 13:40–51.

HELFMAN, G. S. 1978. Patterns of community structure in fishes: summary and overview. Env. Biol. Fish. 3:129–148.

______. 1979a. Twilight activities of yellow perch (*Perca flavescens*). J. Fish. Res. Board Can. 36:173–179.

______. 1979b. Temporal relationships in a freshwater fish community. Unpublished dissertation. Cornell Univ., Ithaca, New York.

HOBSON, E. S. 1968. Predatory behavior of some shore fishes in the Gulf of California. Bur. Sport Fish and Wildlife, Res. Rept. 73:1–92.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven, Connecticut. 302 pp.

JANSSEN, J. A. 1974. Competition and growth of bluegills, green sunfish, and their hybrids and the possible role of aggressive behavior. Unpublished dissertation. Michigan State Univ., East Lansing. 66 pp.

KEAST, A. 1978. Tropic and spatial interrelationships in the fish species of an Ontario temperate lake. Env. Biol. Fish. 3:7–31.

KEAST, A., AND L. WELSH. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. 25:1133–1144.

KELSO, J. R. M., AND F. J. WARD. 1977. Unexploited percid populations of West Blue Lake, Manitoba, and their interactions. J. Fish. Res. Board Can. 34:1655–1669.

LARKIN, P. A. 1956. Interspecific competition and population control in freshwater fish. J. Fish. Res. Board Can. 13:327–342.

LAWLER, G. H. 1969. Activity periods of some fishes in Heming Lake, Canada. J. Fish. Res. Board Can. 26:3266–3267.

MCCRIMMON, H. R. 1968. Carp in Canada. Fish. Res. Board Can., Bull. 165. 93 pp.

MCNAUGHT, D. C., AND A. D. HASLER. 1961. Surface schooling and feeding behavior in the white bass, (*Roccus chrysops*) (*Rafinesque*) in Lake Mendota. Limnol. Oceanogr. 6:53–60.

MILLER, H. J., C. L. BRYDNILDSON, AND C. W. THREINEN. 1959. Rough fish control. Wisconsin Conserv. Dept. Publ. No. 229. 15 pp.

NURSALL, J. R. 1973. Some behavioral interactions of spot-tail shiners (*Notropis hudsonius*), yellow perch (*Perca flavescens*) and northern pike (*Esox lucius*). J. Fish. Res. Board Can. 30:1161–1178.

OLMSTEAD, L. L., AND R. V. KILAMBI. 1971. Interrelationships between environmental factors and feeding biology of white bass of Beaver Reservoir, Arkansas. Pages 398–509 *in* G. E. Hall, ed., Reservoir fisheries and limnology, Amer. Fish. Soc. Special Pub. No. 8.

PYKE, G. H., H. R. PULLIMAN, AND E. L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52:137–154.

SCOTT, D. C. 1955. Activity patterns of perch, *Perca flavescens*, in Randeau Bay of Lake Erie. Ecology 36:320–327.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Fish. Res. Board Can. Bull. 184:1–920.

SHIOZAWA, D. K. 1975. The population dynamics of *Tanypus stellatus* Coquillett (Diptera: Chironomidae) in Goshen Bay of Utah Lake. Unpublished thesis. Brigham Young Univ., Provo, Utah. 22 pp.

SHIOZAWA, D. K., AND J. R. BARNES. 1977. The microdistribution and population trends of larval *Tanypus stellatus* Coquillett and *Chironomus frommeri* Atchley and Martin (Diptera: Chironomidae) in Utah Lake, Utah. Ecology 58:610–618.

TILLMAN, D. L., AND J. R. BARNES. 1973. The reproductive biology of the leech *Helobdella stagnalis* L. in Utah Lake, Utah. Freshwat. Biol. 3:137–145.

TRAPNELL, F. E. 1969. Age and growth of white bass, (*Roccus chrysops*) (Rafinesque), in Mud Lake, near Provo, Utah. Unpublished thesis. Brigham Young Univ., Provo, Utah. 29 pp.

VINYARD, G. L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (*Lepomis macrochirus*) and pumpkin seed (*L. gibbosus*) predation. Can. J. Fish and Aq. Sci. 37:2294–2299.

WERNER, E. E., AND D. J. HALL. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052.

______. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science 191:404–406.

______. 1977. Competition and habitat shift in two sunfishes (*Centrarchidae*). Ecology 58:869–876.

______. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60:256–264.

WERNER, E. E., D. J. HALL, D. R. LAUGHLIN, D. J. WAGNER, L. A. WILSMANN, AND F. C. FUNK. 1977. Habitat partitioning in a freshwater fish community. J. Fish. Res. Board Can. 34:360–370.

WERNER, E. E., G. G. MITTELBACH, AND D. J. HALL. 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. Ecology 62:116–125.

DISTRIBUTIONAL RECORDS FOR THE COLORADO FLORA II.

D. Wilken[1] and J. S. Peterson[2]

Abstract.— Eight new records of vascular plants indigenous to North America and one significant range extension are reported for the flora of Colorado.

The following collections document new records for vascular plants as treated by Harrington (1954), Weber and Johnston (1976), and Weber and Wittman (1983). Herbarium citations follow the treatment by Holmgren and Keuken (Index Herbariorum, Ed. 6, 1974). We thank Noel Holmgren and Rupert Barneby for their expert aid in providing names for several of these collections.

***Astragalus jejunus* S. Watson.** Moffat Co.: Vermillion Creek, 2.3 miles directly E of Vermillion Creek Gap, T10N R100W S33, 6800 ft, 8 Jun 1983, J. S. Peterson and K. Wiley-Eberle 83-141 (COLO, CS, RM). This site extends the known distribution south from Sweetwater Co., Wyoming, and east from Summit Co., Utah (Barneby 1964, Welsh and Moore 1965).

***Astragalus nelsonianus* Barneby.** Moffat Co.: Powder Wash, 2 miles E-SE of the community of Powder Wash, T11N R97W S10, 6820 ft, 21 June 1983, J. S. Peterson and D. H. Wilken 83-232 (CS, NY). This site extends the known distribution south from Sweetwater Co., Wyoming (Barneby 1964).

***Collomia grandiflora* Dougl. ex Lindl.** Rio Blanco Co.: 0.8 mile E-SE of jct of Cow Creek and West Branch, Cow Creek, T4S R94W S18, 2340 m, 8 July 1982, W. Kelley and S. Sigstedt 82-87 (COLO, CS). Garfield Co.: East Fork, Middle Stuart Gulch, 2.6 miles S of Rio Blanco Co. line, T4S R96W S32, 2438 m, 12 July 1982, R. Popp and M. Waters 82-368 (CS). These collections confirm the earlier report by Graham (1937) of the species in the Piceance Basin and extend the known distribution in Colorado north from Mesa Verde and Sleeping Ute Mt. in Montezuma Co. (Welsh and Erdman 1964; W. A. Weber, West Slope Flora, unpubl. ms.).

***Eriogonum acaule* Nuttall.** Moffat Co.: 2 miles NE of confluence of Shell Creek and Hells Canyon, T12N R99W S21, 6820 ft, 8 June 1983, J. S. Peterson and A. Deardorff 83-131 (COLO, CS). SE end of Cold Springs Mt., Co. Rd. 10, 2.2 miles NE of Co. Rd. 318, T9N R101W S5, 6100 ft, 4 June 1979, R. Hartman and B. E. Nelson 8847 (RM). These sites extend the known distribution south from Sweetwater Co., Wyoming.

***Gentianella tortuosa* Jones.** Rio Blanco Co.: Cathedral Bluffs at head of Dry Gulch, T3S R99W S29, 2591 m, 2 September 1982, W. Baker and T. Naumann 82-329 (COLO, CS). Cathedral Bluffs, 3 miles SE of jct of Right and Middle forks, Tommys Draw, T3S R100W S13, 21 July 1982, W. Kelley and T. Naumann 82-149 (CS). These sites extend the known distribution east from Grand and Uintah cos., Utah.

***Penstemon gibbensii* R. Dorn.** Moffat Co.: Brown's Park, 0.7 km S of Sterling Spring, 1707 m, 20 July 1978, J. S. Peterson et al. 1261 (CS, NY). This specimen compares well with the holotype (RM) in all respects and represents an extension south from the type locality in Sweetwater Co., Wyoming (Dorn 1982).

***Sphaeromeria capitata* Nuttall.** Moffat Co.: Vermillion Bluffs, 3 miles NE of summit of Lookout Mt., T11N R98W S30, 7600 ft, 24 June 1983, J. S. Peterson and D. H. Wilken 83-301 (BRY, COLO, CS, RM, UTC). This site extends the known distribution south from Albany and Sweetwater cos., Wyoming (Holmgren et al. 1976).

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Townsendia strigosa **Nuttall.** Moffat Co.: Dry Creek, 1.5 miles W of summit of Lookout Mt., T11N R99W S33, 6580 ft, 22 June 1983, J. S. Peterson and D. H. Wilken 83–287 (CS). This site extends the known distribution east from Uintah Co., Utah (Beaman 1957).

Trifolium andinum **Nuttall.** Moffat Co.: Vermillion Creek Gap, 1.5 miles SE of S entrance to Irish Canyon, T10N R101W S35, 6000 ft, 3 June 1983, J. S. Peterson and A. Deardorff 83–91 (COLO, CS). This site extends the known distribution east from Dagget and Summit cos., Utah (Welsh 1978).

Literature Cited

Barneby, R. 1964. Atlas of North American *Astragalus*. Memoirs New York Botanical Garden 13(1):1–596.

Beaman, J. 1957. The systematics and evolution of *Townsendia* (Compositae). Contrib. Gray Herbarium 183:1–151.

Dorn, R. 1982. A new species of *Penstemon* (Scrophulariaceae) from Wyoming. Brittonia 34:334–335.

Graham, E. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. Annals Carnegie Museum 26:1–432.

Harrington, H. D. 1954. Manual of the plants of Colorado. Denver: Sage books.

Holmgren, A. H., L. M. Schultz, and T. K. Lowery. 1976. *Sphaeromeria*, a genus closer to *Artemisia* than to *Tanacetum* (Asteraceae: Anthemideae). Brittonia 28:255–262.

Weber, W. A., and B. C. Johnston. 1976. Natural history inventory of Colorado. 1. Vascular plants, lichens and bryophytes. University of Colorado Museum, Boulder.

Weber, W. A., and R. Wittmann. 1983. Additions to the flora of Colorado. IX. Phytologia 53:191–193.

Welsh, S. L. 1978. Utah Flora: Fabaceae (Leguminosae). Great Basin Nat. 38:225–367.

Welsh, S. L., and J. A. Erdman. 1964. Annotated checklist of the plants of Mesa Verde, Colorado. BYU Sci. Bull., Biol. Ser. 4(4):1–32.

Welsh, S. L., and G. Moore. 1973. Utah plants. Brigham Young Univ. Press, Provo, Utah.

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UTAH FLORA: POLYGONACEAE

Stanley L. Welsh[1]

Abstract.— The genera and species of Polygonaceae in Utah are revised. Descriptions and keys to taxa are included, along with habitat, elevation, and distributional data. Taxonomic problems are outlined and discussed. Described as new is *Eriogonum brevicaule* Nutt. var. *promiscuum* Welsh. New nomenclatural combinations include *Eriogonum batemanii* Jones var. *eremicum* (Reveal) Welsh and var. *ostlundii* (Jones) Welsh; *E. brevicaule* Nutt. var. *desertorum* (Maguire) Welsh, var. *ephedroides* (Reveal) Welsh, var. *loganum* (A. Nels.) Welsh, var. *nanum* (Reveal) Welsh, and var. *viridulum* (Reveal) Welsh; *E. corymbosum* Benth var. *cronquistii* (Reveal) Welsh, var. *humivagans* (Reveal) Welsh, var. *smithii* (Reveal) Welsh; *E. lonchophyllum* T. & G. var. *saurinum* (Reveal) Welsh; *E. nummulare* Jones var. *ammophilum* (Reveal) Welsh; *E. racemosum* Nutt. var. *coccineum* (J. T. Howell) Welsh and var. *zionis* (J. T. Howell) Welsh; *E. spathulatum* Gray var. *natum* (Reveal) Welsh.

The members of the Polygonaceae, especially those in the genera *Eriogonum*, *Polygonum*, and *Rumex*, have consistently been regarded as taxonomically difficult. Flowers are greatly reduced and often similar from taxon to taxon. They have been used to supplement vegetative characters as diagnostic tools. Often, vegetative features are inconstant, and their use has led to frustration in attempts to identify or classify members of this family.

Certainly the most difficult genus is *Eriogonum*, which consists of both annuals and perennials. The annuals are rather well marked, even though distinguished by minute, but mainly consistent, diagnostic features. The perennials pose problems due, in part at least, to hybridization and the tendency of hybrid derivatives to adapt to specialized environments, often limited by edaphic characteristics. Populations on given substrates are often relatively uniform, but they blend at the edges into the parental types. Some of the segregates are sufficiently distinct and geographically correlated as to warrant taxonomic recognition, but others are not. There is a general lack of consistent diagnostic features. Use of single criteria, such as stem pubescence, branching of the inflorescence, or flower color, leads to arbitrarily defined assemblages of specimens that often do not constitute taxa. Apparently similar morphological groupings can be derived quite independently.

Not all groups of perennials suffer from the same problems or to the same extent. *Eriogonum alatum* stands quite apart from other species. The group of species centering around *E. umbellatum*, which has flowers long-attenuated basally, are distinctive. Soil specialists in the pulvinate-caespitose, mound-forming series are remarkably discrete. Major problems occur in the group of acaulescent perennials and shrubs.

Thus, attempts at presentation of a taxonomy that is equivalent to other families is difficult, if not impossible. The taxonomy must, however, reflect the reality of the naturally occuring poppulations. The attempt presented herein depicts a reticulum of interrelated taxa, connected by series of intermediates. Traditional taxonomy is based, largely, on a concept of lineality, where taxa give rise to others through accumulated genetic modifiers. The system of nomenclature is likewise lineal, with names ordered to imply descent in only one direction, i.e., from the next higher category. Taxonomy within the woody and related perennial species of *Eriogonum* does not fit tradition, but is hardly unique. Similar situations occur in such families as the Chenopodiaceae (*Atriplex*) and Cactaceae (*Opuntia*).

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Problems are discussed specifically in the taxa within which they occur.

Polygonum consists of several groups of species, some of which have been regarded at generic rank. The groups are rather easily defined, and the species within each group are obviously related. The most difficult taxonomic problems lie within the *aviculare* section, where taxonomic criteria are not strongly correlated. Introduced Old World species complicate the picture, since only portions of the total variation of the species are represented, and application of names might be tentative.

Rumex consists of both indigenous and introduced taxa. Nature of the inner perianth segments, the valves, has been relied on for diagnostic features. A grainlike tuberosity forms on one or more of the segments in some taxa, or is lacking altogether. The character is not always reliable. However, the taxa are, for the most part, distinctive. Evidence of intermediacy revolves around those plants similar to *R. crispus*, *R. patentia*, and *R. obtusifolius*. The similar *R. occidentalis* is not always readily separable from phases of that group.

Economic importance of the Polygonaceae in Utah is both positive (rhubarb) and negative (black bindweed, knotweed, and dock). The members are of considerable ecological importance, however. Many taxa occupy distinctive habitats, sometimes as the principal component of the vegetation. Others are pioneer species, capable of occupying a large number of habitats. Two species are grown routinely as ornamentals, *Polygonum aubertii*, a twining vine, and *P. cuspidatum*, a large shrublike, herbaceous perennial. Some of the eriogonums are beautiful and show potential for use as ornamentals. Others should be investigated for reclamation potential. Possible use in rehabilitation is suggested by their occupation of harsh substrates such as those associated with coal-bearing strata. Cultural criteria require investigation. *Rumex crispus* is lauded by herbalists as a curative.

The family is large by Utah standards, with 87 species and 27 varieties, or a total of 114 taxa in 6 genera. The largest genus is *Eriogonum*, with 55 species and 26 varieties, or a total of 81 taxa. This study is based on examination of 3480 specimens, with 551 (15.8%) of them collected by me.

Polygonaceae

Annual or perennial herbs, subshrubs, shrubs, or twining vines; leaves simple, alternate, opposite, or whorled; stipules forming a sheath (ocrea) or absent; flowers perfect or polygamo-dioecious, regular; perianth 2- to 6-parted or -cleft; stamens 2–9; styles 2 or 3; ovary superior, 1-loculed, 1-ovuled; fruit an achene.

1. Sheathing stipules lacking; flowers subtended by a campanulate, obconic, or cylindric involucre, or by a folded, 2-toothed bract 2

— Sheathing stipules present; flowers not subtended by an involucre or with a folded, 2-toothed bract 5

2(1). Flowers solitary, subtended by a single, folded, 2-toothed bract, this accrescent and prominently veined in fruit; plants slender, broad-leaved annuals, known from Washington County .... *Pterostegia*

— Flowers solitary (in *Chorizanthe*) or several, arising from a campanulate, obconic, or cylindric involucre; plants various, but not as above 3

3(2). Involucres with lobes or teeth not spiny; bracts unarmed; plants annual, perennial, or shrubby .... *Eriogonum*

— Involucres and bracts armed with spines; plants annual 4

4(3). Involucres with 2 or more flowers, the lobes tipped with straight spines or bristles; main bracts of inflorescence connate-perfoliate, disklike .... *Oxytheca*

— Involucres usually with one flower, the lobes tipped with hooked or straight spines; bracts not both perfoliate and disklike .... *Chorizanthe*

5(1). Leaves all basal, the blades reniform; sepals 4; styles 2; plants of high elevations .... *Oxyria*

— Leaves cauline or basal, but, if basal, the blades not reniform and plants not or seldom of high elevations; sepals 5 or 6; styles 2 or 3; plants variously distributed 6

6(5). Sepals 5 (rarely 4), all similar and erect in fruit .... *Polygonum*

— Sepals 6, in 2 sets, the inner ones erect and winged in fruit, or the wings from the achenes, the outer sepals reflexed and often smaller 7

7(6). Stipular sheathes large and prominent; stamens 8–10; leaf blades ovate to orbicular; plants cultivated and persisting .... *Rheum*

— Stipular sheaths not prominent, evanescent; stamens 6; leaf blades narrower; plants indigenous or adventive, not cultivated .... *Rumex*

CHORIZANTHE R. Br. ex Benth.

Annual herbs; stems more or less dichotomously branched or simple; leaves basal or cauline and alternate, entire, the upper ones often reduced to opposite or whorled bracts; inflorescence cymose or capitate; involucres sessile, cylindric to urn shaped or funnelform, mostly 1-flowered, 3- to 6-angled or -ribbed and 3- to 6-toothed or -cleft, the teeth spreading, armed with straight or recurved awns; flowers pedicellate or subsessile; bractlets lacking; perianth 6-parted or -cleft; stamens 3–9; styles 3; achenes glabrous, 3-angled.

1. Foliar bracts 3-lobed; involucres with 3, broad, horizontally spreading, saccate horns at the base .... *C. thurberi*

— Foliar bracts entire; involucres not horned at the base 2

2(1). Involucres 6-ribbed, the 6 teeth sparingly recurved apically, less than 2 mm long; stems very brittle and soon falling apart; foliage leaves all basal; stem leaves reduced to subulate bracts .... *C. brevicornu*

— Involucres 3-angled, the 3 teeth straight, more than 5 mm long; stems not brittle (the plants persisting and burlike); stems with some foliar leaves like the basal ones .... *C. rigida*

Chorizanthe brevicornu **Torr.** Short Spineflower. Plants erect or ascending, mainly 5–28 cm tall; stems usually several from the base, strigulose, breaking at the nodes when dry; leaves mostly basal, 1–6 cm long, 2–8 mm wide, narrowly oblanceolate, reduced to opposite bracts upward; involucres solitary in axils of branches, subcylindric, conspicuously 6-ridged, straight or curved, ca 4 mm long, the lobes with recurved spinose teeth; flowers 3–4 mm long, glabrous, the perianth lobes whitish, subequal; stamens 3; achenes ca 2 mm long. Creosote bush, blackbrush, and other warm and salt desert shrub communities at 760 to 1220 m in Grand, Kane, San Juan, and Washington counties; Nevada, Arizona, and California; 14 (iv).

Chorizanthe rigida **(Torr.) T. & G.** Rigid Spine-flower. [*Acanthogonium rigidum* Torr.]. Plants erect, mainly 2–9 cm tall;

Stems simple, obscured by bracts and leaf bases; main leaves long-petiolate, the blades 0.8–2 cm long and about as broad, oval to orbicular or obovate, woolly beneath, green and sparingly tomentose above; secondary leaves bracteate, lanceolate to subulate, spine-tipped, indurate and thorny at maturity; inflorescence dense, with involucres clustered in bract axils; tube of involucre ca 2 mm long, 3-angled, with 3 broad, spreading, unequal, straight, spine-tipped lobes 4–12 mm long; perianth yellowish, almost included; stamens 9; achenes ovoid, prominently beaked, ca 2 mm long. Creosote bush, Joshua tree, and other warm desert shrub communities at 760 to 1130 m in Washington County; Arizona, Nevada, California, and Mexico; 8 (i).

Chorizanthe thurberi **(Gray) Wats.** Thurber Spine-flower. [*Centrostegia thurberi* Gray]. Plants erect, usually simple from the basal rosette and typically dichotomously branched upward, 4–16 cm tall; basal leaves 4–30 mm long, 3–6 mm wide, spatulate, subglabrous; foliar bracts 3-lobed, spine-tipped, 2–4 mm long; involucres solitary, borne in branch axils, 4–6 mm long, 5-toothed apically, the teeth armed with straight spines, 3-angled and with 3 saccate, spinose horns near the base; perianth included, pubescent; stamens 6 or 9; achenes ca 1.5 mm long. Creosote bush, blackbrush, mountain brush, and pinyon-juniper communities at 850 to 1700 m in Garfield (?), Kane, and Washington counties; Arizona, Nevada, and California; 12 (i). The report for Garfield County is based on a specimen collected "40 miles south of Boulder, in creosote bush," and might be mislabeled.

ERIOGONUM Michx.

Annual or perennial herbs, subshrubs, or shrubs; leaves basal or cauline and alternate, or with scalelike to foliaceous alternate or whorled bracts, entire, estipulate; flowers perfect or imperfect, borne in campanulate, obconic, or cylindric involucres; involucres 4- to 10-lobed or -toothed, or rarely in 2 whorls or 3 more or less distinct bracts, awnless, few to many flowered, sessile or stipitate; perianth petaloid, 6-segmented, in 2 series; flowers pedicellate, subsessile, or the base attenuated and stipelike; stamens 9, the filaments filiform; ovary 1-loculed, with 3 styles and capitate stigmas; achenes 3-angled or -winged. **Note:** This is a dual genus, consisting of annual species distinguished by minute diagnostic characteristics, and of perennial herbs, subshrubs, and shrubs that are connected through series of intermediates that defy segregation and construction of keys based on characters similar to those used in the annual species. Taxonomic problems are not easily resolved, and the approach presented below is only tentative.

REVEAL, J. L. 1967. Notes on *Eriogonum*—V. A revision of the *Eriogonum corymbosum* complex. Great Basin Nat. 27:183–220.

______. 1969. A revision of the genus *Eriogonum* (Polygonaceae). Unpublished dissertation. Brigham Young Univ. 546 p.

______. 1973. *Eriogonum* (Polygonaceae) of Utah. Phytologia 25:169–217.

REVEAL, J. L., AND B. J. ERTTER. 1976. Reestablishment of *Stenogonum* Nutt. (Polygonaceae). Great Basin Nat. 36:272–280.

HESS, W. J. and J. L. REVEAL. 1976. A revision of *Eriogonum* (Polygonaceae), Subgenus Pterogonum. Great Basin Nat. 36:281–333.

1. Plants annual (except in some *E. inflatum*, q.v.), from slender taproots .... Key I

— Plants perennial herbs, subshrubs, or shrubs 2

2(1). Plants definitely shrubby, the stems developed above ground level and with 1 to several elongated internodes .... Key II

— Plants acaulescent, or, if caulescent, the stems prostrate at ground level or the internodes very short and obscured by a tomentum 3

3(2). Flowers with attenuated, stipelike bases; yellow to reddish yellow or cream; plants often with prostrate-spreading stems .... Key III

— Flowers not with stipelike bases, variously colored; plants seldom with prostrate-spreading stems 4

4(3). Plants pulvinate-caespitose, mound forming; inflorescences mainly 0.5–5 cm tall; leaves less than 1 cm long ... Key IV

— Plants not simultaneously pulvinate-caespitose, mound forming, less than 5 cm tall, and with leaves less than 1 cm long ... Key V

Key I

Plants annual (except in some *E. inflatum*).

1. Involucres angled to strongly ribbed, usually tightly appressed vertically to the stems and always sessile ... 2

— Involucres smooth, not ribbed or angled, usually stipitate, or, if sessile, not vertically appressed to the stems ... 9

2(1). Leaves puberulent to villous beneath, but not tomentose ... 3

— Leaves tomentose, at least beneath ... 5

3(2). Cauline leaves more or less bracteate, the blades not well developed, soft-hairy; involucres 4-lobed; flowers white, suffused with red, glabrous or sometimes hispidulous, 1–1.8 mm long; plants of southwestern Utah .... *E. puberulum*

— Cauline leaves with well-developed blades, variously hairy; involucres 5-lobed; flowers variously colored, 1.5–2 mm long; distribution various ... 4

4(3). Outer perianth segments broadly obovoid, hooded, markedly ciliate, otherwise glabrous; plants of Kane and San Juan counties ... *E. darrovii*

— Outer perianth segments oblong to ovate, not hooded or markedly ciliate, otherwise hispidulous and more or less glandular; plants of central and eastern Utah ... *E. divaricatum*

5(2). Foliage leaves cauline and basal; plants of Kane and Washington counties ... *E. polycladon*

— Foliage leaves all basal; plants variously distributed ... 6

6(5). Stems tomentose to floccose-tomentose ... 7

— Stems glabrous ... 8

7(6). Flowers yellow to red, the outer perianth segments broadly obovate ... *E. nidularium*

— Flowers white, the outer segments narrowly obovate ... *E. palmerianum*

8(6). Involucres 3–5 mm long; achenes ca 2 mm long; plants of Washington County ... *E. davidsonii*

— Involucres 1–2.5 mm long; achenes ca 1 mm long; plants of Beaver County ... *E. baileyi*

9(1). Leaves glabrous or variously pubescent but not tomentose or lanate, even on the lower blade surface ... 10

— Leaves tomentose to lanate on the lower blade surface, at least ... 15

10(9). Involucres in 2 whorls, each whorl 3-lobed ... 11

— Involucre consisting of a single whorl, this usually 4- or 5-lobed ... 12

11(10). Foliage leaves all basal; peduncles abruptly bent above the middle ... *E. flexum*

— Foliage leaves both cauline and basal; peduncles straight or gently curved ... *E. salsuginosum*

12(10). Stems usually strongly inflated; plants of broad distribution, annual or perennial ... *E. inflatum*

— Stems not inflated (except in some *E. trichopes*, q.v.); plants annual, of various distribution ... 13

13(12). Flowers glabrous, white, fading yellowish; plants of eastern Utah ..... *E. gordonii*

— Flowers hairy, yellowish or reddish; plants of western and southwestern Utah 14

14(13). Branches of inflorescence with stipitate, usually purplish glands; flowers densely villous; involucres 5-lobed; plants of western Utah ..... *E. howellianum*

— Branches of inflorescence not glandular; involucres 4-lobed; plants of Washington County ..... *E. trichopes*

15(9). Foliage leaves both cauline and basal 16

— Foliage leaves all basal (except in some *E. cernuum*, q.v.) 17

16(15). Flowers glabrous, yellow, the outer perianth segments cordate-ovate; leaves linear to narrowly oblanceolate ..... *E. pharnaceoides*

— Flowers minutely glandular-puberulent, white to yellowish or pink, the outer segments oval; leaves obovate to lanceolate ..... *E. maculatum*

17(15). Involucres minute, 0.3–1 mm long 18

— Involucres 1–3 mm long 20

18(17). Flowers yellow, soon suffused with red, glabrous; plants of southeastern Utah ..... *E. wetherillii*

— Flowers white to pink or yellow, hairy or glabrous; plants of southwestern Utah 19

19(18). Flowers yellow; outer perianth lobes with saccate-dilated bases, pubescent ..... *E. thomasii*

— Flowers white to pink; outer perianth lobes not swollen at the base, pubescent or glabrous ..... *E. subreniforme*

20(17). Branches of inflorescence or stipes with dark, stipitate glands; plants of Washington County ..... *E. brachypodum*

— Branches of inflorescence or stipes glabrous (or tomentulose), or if stipes glandular (as in *E. nutans*), not of Washington County 21

21(20). Involucres and flowers puberulent and more or less glandular; plants of Washington County ..... *E. pusillum*

— Involucres and flowers glabrous (or tomentulose); plants variously distributed 22

22(21). Branches of inflorescence more or less tomentose (at least when young) and glandular; leaf margins conspicuously undulate-crisped; plants of eastern Utah ..... *E. scabrellum*

— Branches of inflorescence glabrous; leaf margins not especially undulate; plants variously distributed 23

23(22). Outer perianth segments merely truncate to obtuse basally; involucres usually stipitate 24

— Outer perianth segments cordate at the base; involucres usually sessile 25

24(23). Stipes glabrous; outer perianth segments violin shaped, constricted below the middle, the margins undulate, more or less saccate below; plants common and widespread ..... *E. cernuum*

— Stipes stipitate-glandular; outer segments obovate, not constricted below the middle, the margins not especially saccate; plants uncommon ..... *E. nutans*

25(23). Involucres erect on branches of inflorescence; plants of Iron and Washington counties ..... *E. insigne*

— Involucres deflexed on branches of inflorescence; plants of various distribution 26

26(25). Involucres broadly campanulate, broader than long; flowers yellow to reddish yellow; plants widespread .... *E. hookeri*

— Involucres obconic, somewhat longer than broad; flowers white to pink; plants of western and southern Utah .... *E. deflexum*

KEY II

Plants definitely shrubby.

1. Flowers pubescent, white to pink; leaves fascicled in at least some axils; plants of Washington County .... *E. fasciculatum*

— Flowers glabrous, variously colored; leaves fascicled or not; plants variously distributed 2

2(1). Stems angled or ribbed and more or less grooved, or conspicuously flexuous; plants of Washington County 3

— Stems rounded or terete and not especially, if at all, flexuous; plants variously distributed 4

3(2). Stems both flexuous and grooved, usually glabrous; involucres 0.7–1.5 mm long .... *E. heermannii*

— Stems flexuous, almost terete, tomentose; involucres 2–2.5 mm long; plants not known in contemporary collections from Utah [*E. palmeri* Wats., type from Washington County] .... *E. plumatella* Dur. & Hilg.

4(3). Plants completely glabrous; plants of Emery and Wayne counties ..... *E. corymbosum*

— Plants pubescent or tomentose, variously distributed 5

5(4). Leaves oval to oblong or elliptic, mostly less than 3 times longer than broad 6

— Leaves linear to narrowly oblong or narrowly elliptic, mostly 5–10 times longer than broad 9

6(5). Flowers not much exserted from the involucres; leaves typically densely tomentose on both surfaces; plants mainly of the Great Basin and western Kane and eastern Washington counties .... *E. nummulare*

— Flowers conspicuously exserted from the involucres; leaves often only thinly tomentose above; plants of broad distribution 7

7(6). Inflorescences ca half as long as plant height, about equaling the leafy portion of current annual growth; involucres racemosely arranged; plants of Washington County .... *E. wrightii*

— Inflorescences usually much less than one-forth the plant height; plants variously distributed 8

8(7). Leaf apices acute, the blades mostly elliptic and more or less revolute, mainly less than 8 mm wide; plants widespread .... *E. microthecum*

— Leaf apices typically rounded, the blades orbicular to oblong or ovate to obovate, seldom, if at all, revolute, mainly more than 8 mm wide ...... *E. corymbosum*

9(5). Leaves flat, slightly, if at all, revolute 10

— Leaves revolute, the lower surface largely obscured by revolute margins 12

10(9). Plants semishrubby only; stems of current growth dying to plant base ... *E. brevicaule*

— Plants definitely shrubby; stems of current growth not dying to plant base each year 11

11(10). Leaves with margins at least somewhat revolute; plants broadly distributed .... *E. corymbosum*

— Leaves mainly flat; plants of northern Uintah County .... *E. lonchophyllum*

12(9). Inflorescences mainly 8–20 cm long or more; involucres racemose; plants of sandy tracts in the Navajo Basin .... *E. leptocladon*

— Inflorescences mainly 1–6 cm high; involucres cymose; plants variously distributed, but usually not in deep sand 13

13(12). Plants low, mat forming; flowers bicolored, pink and white .... *E. bicolor*

— Plants low to tall, but not mat forming; flowers white, pink, reddish, or yellow 14

14(13). Flowers yellow; plants of clay and silt substrates in eastern Grand County .... *E. contortum*

— Flowers white, pink, or reddish; plants variously distributed 15

15(14). Leaf axils (at least some) with fascicled leaves; plants of San Juan County .... *E. clavellatum*

— Leaf axils seldom with fascicled leaves (if ever); plants of various distribution 16

16(15). Leaves mainly 3–7 cm long; involucres clustered on inflorescence branch tips; plants of Duchesne County, and sometimes elsewhere .... *E. corymbosum*

— Leaves mainly 0.8–3 cm long; involucres not clustered; plants widespread .... *E. microthecum*

KEY III

Flowers with attenuated, stipelike bases.

1. Stems with whorled, foliose bracts near the middle; plants of northern Utah .... *E. heracleoides*

— Stems lacking whorled bracteate leaves, or these closely subtending the plants inflorescences; variously distributed 2

2(3). Flowers glabrous .... *E. umbellatum*

— Flowers hairy 3

3(2). Stems with whorled bracteate leaves subtending the umbellate inflorescence; involucres to 6 mm wide or more .... *E. jamesii*

— Stems lacking whorled bracteate leaves subtending the capitate inflorescence; involucres to 3 mm wide .... *E. caespitosum*

KEY IV

Plants pulvinate caespitose, mound forming;
inflorescences less than 5 cm tall and leaves less than 1 cm long.

1. Leaf blades oval, almost or quite as broad as long .... *E. ovalifolium*

— Leaf blades longer than broad 2

2(1). Scapes, if present, glabrous; plants of central and south central Utah . *E. panguicense*

— Scapes, if present, tomentose; plants of various distribution 3

3(2). Flowers glabrous, 2–3 mm long; plants of San Francisco Range .... *E. soredium*

— Flowers hairy, mainly 2–4 mm long; distribution various 4

4(3). Ovaries and achenes pubescent; flowers white or yellow; plants of lower elevations in Great Basin and in eastern Utah .... *E. shockleyi*

— Ovaries and achenes glabrous; flowers yellow, white, or pink; plants variously distributed 5

5(4). Heads 10–15 mm wide, usually evidently pedunculate, and definitely bracteate; plants mainly of the Great Basin .... *E. villiflorum*

— Heads less than 10 mm wide, usually sessile and not evidently bracteate; plants of eastern and south central Utah 5

6(5). Flowers white to rose, 3.5–4 mm long; involucres 6- to 8-lobed; plants of eastern Utah .... *E. tumulosum*

— Flowers yellow 1.8–2.5 mm long; involucre 4-lobed; plants of Garfield County .... *E. aretioides*

KEY V

Plants herbaceous perennials with leaves more than 1 cm long
and with stems or scapes more than 5 cm tall.

1. Caudex branches or root crown 1–2.5 cm thick, clothed with persistent leaf bases, these with persistent, coarse, villous-pilose hairs; plants wandlike, mainly 3–12 dm tall .... *E. alatum*

— Caudex branches or root crown less than 1 cm thick, or, if thicker, not villous-pilose 2

2(1). Inflorescence racemose or paniculate, the involucres spaced along elongate, erect branches .... *E. racemosum*

— Inflorescence cymose, the involucres clustered on short, spreading branches 3

3(2). Leaf blades all oval to orbicular and about as broad as long; inflorescence branching or capitate, but if the latter the inflorescence mostly 15–30 mm wide 4

— Leaf blades, at least some, much longer than broad, or, if as above, the inflorescence capitate and 5–14 mm wide 5

4(3). Involucres capitate; flowers white, pink, or yellow; plants widespread *E. ovalifolium*

— Involucres borne in open cymes; flowers white or pink; plants of central to western Utah .... *E. batemanii*

5(3). Plants strictly acaulescent above caudex branches 6

— Plants short-caulescent, the internodes apparent, though short and obscured by dense tomentosum, or, if acaulescent, the inflorescence branched 7

6(5). Scapes glabrous; flowers white; plants mainly of southern highlands .. *E. panguicense*

— Scapes tomentose; flowers white, pink, cream, or yellow .... *E. brevicaule*

7(6). Scapes or peduncles pubescent, or, if glabrous (as in some *E. spathulatum*), the plants of Beaver County 8

— Scapes or peduncles glabrous; plants variously distributed 9

8(7). Involucres capitate; plants of northern Utah .... *E. brevicaule*

— Involucres in branching cymes or subcapitate; plants of central and western Utah .... *E. spathulatum*

9(7). Flowers yellow; involucres not in capitate clusters; leaves linear to lanceolate or oblanceolate .... *E. brevicaule*

— Flowers white or pink; leaves oblong to elliptic or ovate-lanceolate 10

10(9). Leaves broadly elliptic to ovate-lanceolate, the blades usually less than 3 times longer than broad .... *E. batemanii*

— Leaves narrowly elliptic, commonly 5–8 times longer than broad .. *E. lonchophyllum*

Eriogonum alatum **Torr. in Sitgr.** Winged Buckwheat. [*E. triste Wats., type from Kane County; E. alatum* ssp. *triste* (Wats.) Stokes]. Perennial herbs, mainly 3–12 dm tall, from a taproot and thick rootcrown, this 1–3 cm thick or more and clothed with persistent, coarsely villous pilose leaf bases, the pith chambered; leaves mainly 3–12 (20) cm long, 3–15 mm wide, narrowly oblanceolate to lanceolate, strigose on one or both surfaces; cauline leaves reduced upward; inflorescence cymose-paniculate; stipes erect, 3–20 mm long; involucres obconic to campanulate, 2–4.5 mm long, pilosulose to glabrous, 5-lobed; perianth yellowish to greenish, 1.5–2.8 mm long, the segments oblong, united to about the middle; achenes 5–9 mm long, 3–6 mm wide, glabrous, 3-winged the entire length. Sagebrush, mixed desert shrub, pinyon-juniper, and mountain brush communities at 1155 to 2685 m in Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Kane, San Juan, Sevier, Uintah, Wasatch, and Wayne counties; Wyoming to Nebraska, south to Arizona, New Mexico, Texas, and Mexico; 66 (x).

Eriogonum aretioides **Barneby** Widtsoe Buckwheat. Pulvinate-caespitose, mound-forming, herbaceous perennials from a pluricipital caudex and woody taproot, the caudex branches mainly 20–50 the taproot clothed with shreddy castaneous to blackish bark; leaves 1–3.5 mm long, 0.8–1.2 mm wide, oblanceolate in outline, revolute, the lower surface obscured, white-pilose, sessile; inflorescence of solitary, sessile involucres, not borne above the rosettes, these campanulate, 2.8–3.2 mm long, 2–4 mm wide, villous, 4-lobed; flowers yellow, 2–2.2 mm long, pilose, the segments lance-ovoid; achenes brown, ca 2 mm long, glabrous. Bristlecone pine, ponderosa pine, Douglas fir, and Rocky Mountain juniper communities, on the Pink Limestone Member of the Wasatch Formation, at 2255 to 2655 m in Garfield (type from near Widtsoe) County; endemic; 5 (0).

Eriogonum baileyi **Wats.** Bailey Buckwheat. Annual herbs, mainly 10–30 cm tall; leaves all basal; blades orbicular or obovate, mainly 5–20 mm long and about as broad, tomentose on one or both sides; petioles 5–30 mm long; inflorescences much-branched, spreading; involucres sessile, subcylindric, 1.5–2.5 mm long, 5-lobed, glabrous, vertically appressed; flowers white to pink, 1.5–2 mm long, glabrous, the outer segments oblong to obovate, slightly constricted near the middle, the inner segments narrower; achenes brown, ca 1 mm long. Sagebrush-rabbitbrush and mountain mahogany communities at 1830 to 2200 m in Beaver County; Oregon and Idaho, south to Nevada and California; 2 (ii).

Eriogonum batemanii **Jones** Bateman Buckwheat. Perennial herbs, mainly 10–45 cm tall; leaves all basal; blades 1–3.5 cm long, 5–16 mm wide, oval, orbicular, elliptic, or lance-oblong, tomentose on one or both surfaces, flat marginally, obtuse to rounded apically; petioles 8–25 mm long; inflorescences usually glabrous, open, cymose-paniculate, the branches spreading-ascending; involucres sessile, clustered or solitary, narrowly campanulate or obconic, 2–4 mm long, with 5, hyaline, rounded lobes; flowers white, 1.5–2.8 mm long, glabrous, the outer segments obovate, the inner ones slightly narrower; achenes brown, 2.5–3 mm long. Three rather weak but geographically correlated varieties occur in Utah.

1. Leaf blades mainly 2-3 times longer than broad; plants of eastern Utah .... *E. batemanii* var. *batemanii*

— Leaf blades about as broad as long; plants of western and central Utah 2

2(1). Involucres capitate, mainly 2–5, terminating long naked branches; plants of western Millard and Beaver counties .... *E. batemanii* var. *eremicum*

— Involucres cymose, mainly 1–5 in branching terminal cymes on rather short branches; plants of Piute and Sevier counties .... *E. batemanii* var. *ostlundii*

Var. ***batemanii*** Mixed desert shrub and pinyon-juniper communities at 1615 to 2515 m in Carbon (type from Price Valley), Duchesne, Emery, Garfield, and Uintah counties; Colorado; 41 (viii). This is a Colorado Plateau endemic. Plants with both capitate and cymose involucres in the branched inflorescences and very short broad leaf blades occur in this entity. Thus, the variation is similar to that represented in the two following varieties, which are distinguished on features not exclusive with them. A specimen from Horn Mountain, Emery County (Foster 8257 BRY), simulates *E. lonchophyllum* var. *lonchophyllum*, and suggests a relationship between *E. batemanii* and that taxon.

Var. *eremicum* (Reveal) Welsh comb. nov. [based on: *E. eremicum* Reveal Phytologia 23: 165. 1972]. Hermit Buckwheat. Shadscale, desert shrub, and juniper communities at 1555 to 1925 m in Beaver and Millard (type from SE of Garrison) counties; endemic; 12 (viii). Substrates include limestone and dolomite. Specimens herein assigned to *E. spathulatum* (q.v.), but having glabrous inflorescences, appear to be intermediate toward this variety.

Var. *ostlundii* (Jones) Welsh comb. nov. [based on: *E. ostlundii* Jones Contr. W. Bot. 11: 12. 1903; *E. spathuliforme* Rydb., type from Piute County]. Elsinore Buckwheat. Shadscale, mixed desert shrub, juniper, and ponderosa pine communities, often on igneous gravels, at 1675 to 1985 m in Piute and Sevier (type from near Elsinore) counties; endemic; 27 (iii).

***Eriogonum bicolor* Jones** Pretty Buckwheat. [*E. microthecum* ssp. *bicolor* (Jones) Stokes]. Mound-forming shrubs, mainly 2–8 cm tall, the horizontal spreading stems mainly 5–20 cm long; leaves caulescent, mostly 5–15 mm long, 1–3 mm wide, clavate, the lower surface more or less obscured by revolute margins, tomentose; current stems white-tomentose; inflorescence umbellate-cymose, on peduncles 3–15 mm long; involucres obconic to broadly campanulate, 2–4 mm long, tomentose to glabrous, with 5 acutish to rounded lobes; flowers white to pink or rose, the midveins often pink to red-purple, 2.2–4 mm long, glabrous, the outer segments obovate to orbicular, the inner ones oblanceolate to elliptic; achenes brown, 3–3.5 mm long. Shadscale, mat-atriplex, other salt and mixed desert shrub, and pinyon-juniper communities at 1340 to 1985 m in Carbon, Emery, Garfield, Grand (type from Thompsons Springs), San Juan, Sevier, and Wayne counties; endemic; 54 (vi).

***Eriogonum brachypodum* T. & G.** Parry Buckwheat. [*E. parryi* Gray, type from St. George; *E. deflexum* ssp. *parryi* (Gray) Stokes; *E. deflexum* var. *brachypodum* (T. & G.) Munz; *E. deflexum* ssp. *brachypodum* (T. & G.) Stokes]. Annual herbs, mainly 5–30 cm tall; leaves all basal, the blades 0.8–4 cm long and about as wide or wider, orbicular to reniform, white-tomentose, at least beneath; inflorescences umbellate, the branches glandular; involucres on stipes 3–15 mm long, usually deflexed, glandular; involucres 1–2.5 mm long, obconic to campanulate, usually glandular, with 5 triangular-acute teeth; flowers white or suffused with red, 1.5–2.8 mm long, glabrous, the outer segments ovate-cordate, the inner ones oblanceolate; achenes brown, 1.5–2 mm long. Creosote bush, other warm desert shrub, and shadscale communities at 760 to 1550 m in Sevier and Washington counties; California, Nevada, and Arizona; 16 (ii).

***Eriogonum brevicaule* Nutt.** Shortstem Buckwheat. Plants perennial; stems of the year dying to the base, mainly 3–40 cm tall, glabrous or tomentose; leaves all basal or some with obvious short stems, the short internodes obscured by a tomentum, 0.3–10 cm long, 1–9 mm wide, tomentose on one or both surfaces, flat to revolute, entire or undulate, linear to elliptic, oblanceolate, or lanceolate; petioles 1–40 mm long; inflorescences cymose, capitate, or cymose-umbellate; involucres solitary or clustered, obconic to campanulate, 1.5–4.5 mm long, tomentose to glabrous, with 5 acute lobes; flowers yellow to cream, white, or suffused with pink, glabrous, the segments ovate to oblong, lanceolate, oval, or obovate; achenes 1.5–3.5 mm long, brown. The *brevicaule* complex typifies the problematical nature of interpretation of perennial members of the genus. Floral morphology is sufficiently reduced and uniform as to lack definitive diagnostic criteria in most instances. Inflorescence structure is only somewhat more useful, but is often variable within a population, ranging from capitate to branched. Flower color is useful in a general sense only, often varying from white to yellow or even pink within a population. Pubescence appears, at first, to be of substantial value, but the use of this criterion fails also. The attempt here is to bring together those members of the group as they occur in Utah, meanwhile acknowledging the problems of recognition of all specimens within a constituent entity. Further, an indication of intermediacy, whether phenotypic, due to ecological response, or genotypic, due to hybridization, is presented. Phenotypic variation in response to different, often subtle, environmental conditions are apparently great. However, some part of the variation is due to hybridization of phases of this complex among themselves and with phases of the *E. corymbosum*, *E. lonchophyllum*, *E. microthecum*, and possibly other complexes. The following treatment should be regarded as tentative at best.

1. Inflorescences branched from well below the middle of the plant height; plants of the southern Uinta Basin .... *E. brevicaule* var. *ephedroides*

— Inflorescence capitate and unbranched or branched from above the middle of the plant height (seldom below in some var. *viridulum*, q.v.) 2

2(1). Leaves revolute, the lower surface completely obscured by the margin; plants of the northern and western Uinta Basin .... *E. brevicaule* var. *viridulum*

— Leaves revolute or flat, the lower surface readily apparent, or, if not, the plants of other distribution 3

3(2). Leaves both flat and scapes monocephalous; plants of northern Utah 4

— Leaves revolute, or, if flat, plants usually with a branching inflorescence 5

4(3). Plants strictly acaulescent; plants of western Box Elder County .... *E. brevicaule* var. *desertorum*

— Plants short-caulescent, the internodes obscured by a white tomentum; plants of Cache, Morgan, and Rich counties .... *E. brevicaule* var. *loganum*

5(3). Plants with a definitely woody caudex, this clothed with black, marcescent leaf bases; leaves usually undulately partially revolute; typically growing in crevices or ridge crests .... *E. brevicaule* var. *nanum*

— Plants with subligneous caudex, this only sometimes with blackish marcescent leaf bases; leaves various, but sometimes as above; of various habitats 6

6(5). Stems glabrous, the inflorescences branching in the upper one-third to one-forth; plants transitional with the following .... *E. brevicaule* var. *brevicaule*

— Stems tomentose, or, if glabrous, inflorescence branching in the upper one-fourth 7

7(6). Flowers white, suffused with pink, or yellow, borne in capitate or branched inflorescences; plants of Minnie Maud Creek and Mt. Bartles vicinity .... *E. brevicaule* var. *promiscuum*

— Flowers usually yellow, borne in capitate or branched inflorescences; plants broadly distributed .... *E. brevicaule* var. *laxifolium*

Var. *brevicaule* [*E. campanulatum* Nutt.; *E. confertiflorum* var. *stansburyi* Benth. in DC., type from Utah; *E. brevicaule* var. *aureum* Benth. in DC.; *E. nudicaule* ssp. *garrettii* Stokes, type from near Echo Reservoir; *E. nudicaule* ssp. *parleyense* Stokes, type from Parleys Canyon]. Sagebrush, juniper, mountain brush, pinyon-juniper, aspen, and spruce-fir communities at 1460 to 2745 m in Daggett, Davis, Salt Lake, Summit, and Utah counties; Idaho, Wyoming, and Colorado; 60 (viii). This variety, as interpreted here, includes var. *wasatchense* (Jones) Reveal [*E. wasatchense* Jones, type from American Fork Canyon], a narrow-leaved phase completely transitional with more typical var. *brevicaule* northward. The narrow-leaved phase is also transitional with var. *laxifolium* (q.v.) southward, and both varieties *brevicaule* and *laxifolium* intergrade upward with the aggregation of forms treated herein as var. *nanum* (q.v.). Hybrids between var. *brevicaule* and *E. corymbosum* are known from Wyoming.

Var. *desertorum* (Maguire) Welsh comb. nov. [based on: *E. chrysocephalum* ssp. *desertorum* Maguire in Maguire & Holmgren Leafl. W. Bot. 3: 11. 1941; *E. desertorum* (Maguire) R. J. Davis]. Desert Buckwheat. Sagebrush, bitterbrush, and juniper communities at ca 1585 to 2440 m in Box Elder County; Nevada; 3 (0). This variety simulates the capitate phase of var. *laxifolium* differing conspicuously only in the flat leaf blades.

Var. *ephedroides* (Reveal) Welsh comb. nov. [based on: *E. ephedroides* Reveal Madrono 19: 295. 1968]. Ephedra Buckwheat. Shadscale, thistle, mixed desert shrub, and open pinyon-juniper communities, on Green River Formation, at 1525 to 2075 m in Uintah (type from south of Bonanza) County; endemic; 28 (iii). This most distinctive phase of the *brevicaule* complex forms apparent hybrids with *E. corymbosum* in the eastern part of its range.

Var. *laxifolium* (T. & G.) Reveal Varying Buckwheat. [*E. kingii* var. *laxifolium* T. & G, type from Wasatch Mts.; *E. chrysocephalum* Gray; *E. chrysocephalum* var. *angustum* Jones, type from Johnson Pass, Tooele County; *E. nudicaule* ssp. *angustum* (Jones) Stokes; *E. brevicaule* var. *pumilum* Stokes ex Jones, type from Carbon County; *E. nudicaule* ssp. *pumilum* (Stokes) Stokes; *E. tenellum* ssp. *cottamii* Stokes, type from Utah County; *E. brevicaule* var. *cottamii* (Stokes) Reveal; *E. medium* Rydb, type from Mt. Nebo]. Mountain brush, sagebrush, pinyon-juniper, ponderosa pine, and aspen communities at 1645 to 3390 m in Duchesne, Emery, Juab, Millard, Salt Lake, Sanpete, Sevier, Tooele, and Utah counties; endemic; 64 (xv). This variety consists of plants with both capitate and open inflorescences, slender to broad leaves, revolute to flat leaves, usually tomentose (but sometimes glabrous) inflorescences, and other diversity. The var. *cottamii* is based on the densely tomentose plants of western ranges, but these are transitional completely at higher elevations with other phases of var. *laxifolium*, and show affinity with *E. spathulatum* (q.v.) downward. Apparent hybrids occur with *E. lonchophyllum* (see var. *promiscuum*).

Var. *loganum* (A. Nels.) Welsh comb. nov. [based on: *E. loganum* A. Nels. Bot. Gaz. 54: 149. 1912; *E. chrysocephalum* ssp. *loganum* (A. Nels.) Stokes]. Logan Buckwheat. Sagebrush-bunchgrass communities at 1460 to 2045 m in Cache (type from Logan), Morgan, and Rich counties; endemic; 8 (0). This material differs only superficially from var. *nanum*, a higher-elevation phase with similar well-developed woody base.

Var. *nanum* (Reveal) Welsh comb. nov. [based on: *E. nanum* Reveal Phytologia 25: 194. 1973; *E. grayi* Reveal, type from Lake Blanche, Salt Lake County]. Dwarf Buckwheat. Sagebrush, mountain brush, spruce-fir, and alpine tundra communities, in crevices in limestone or quartzite outcrops, or on windswept ridges or in talus slopes at 2010 to 3510 m in Box Elder (type from Willard Peak), Cache, Juab, Millard, Salt Lake, Tooele, Utah, and Weber counties; endemic; 35 (i). This assemblage consists of crevice plants and other dwarf, high elevation phases that apparently do not have genetic integrity. Their recognition at any taxonomic rank is, therefore, problematical, and they are treated here for convenience only.

Var. *promiscuum* Welsh var. nov. Similis *Eriogono brevicauli* var. *nano* in floribus varicoloribus — albis, roseis, vel flavis, inflorescentiis simplicibus vel furcatis et foliis involutis vel planis sed in foliis longioribus et revolutis consistans differt. Type. USA. Utah. Carbon County; T13S, R14E, S7, ca 25 mi E of Helper, summit of Mt. Bartles, 3060 m, open ridge top, Green River Formation, 10 Aug. 1977, S. Welsh & S. Clark 15905 (Holotype BRY; Isotypes 10, distributed previously as *Eriogonum*). Additional specimens: Utah. Carbon County; head of Harmon Canyon, ca halfway between Mt. Bartles and Nine Mile Canyon, 18 July 1978, E. Neese & L. England 6160, 6161, 6162, 6163, 6164 (all BRY); near head of Soldier Canyon, 12 Aug. 1967, S. Welsh & E. Christensen 6625, 6626 (BRY); do 15 Aug. 1966, N. H. Holmgren & J. L. Reveal 3015 (BRY); Duchesne County, Gate Canyon, Myton-Wellington road, 25 July 1978, J. S. Peterson & E. Neese 1286 (BRY). The Mt. Bartles buckwheat is similar in some respects with var. *nanum* but appears to have a separate origin. The plants seem to have arisen through hybridization of portions of *E. brevicaule* var. *laxifolium* with *E. corymbosum* var. *hylophilum* and with a possible infusion of *E. lonchophyllum* var. *lonchophyllum*. Flowers are predominantly white suffused with pink, and in the upper elevational reaches have capitate inflorescences. Downward the inflorescences are branched and the plants are transitional to *E. corymbosum*. Yellow-flowered individuals give evidence of contribution from *E. brevicaule* var. *laxifolium*; 12 (iii).

Var. *viridulum* (Reveal) Welsh comb. nov. [based on: *E. viridulum* Reveal Proc. Utah Acad. Sci. 42: 287. 1966]. Duchesne Buckwheat. Pinyon-juniper, shadscale, and mixed desert shrub communities at 1555 to 2135 m in Duchesne (type from 8 mi E of Duchesne) and Uintah counties; endemic; 58 (v). Hybrids between var. *viridulum* and *E. corymbosum*, which simulate *E. corymbosum* var. *aureum*, are locally common in Duchesne and eastern Utah counties. They have been described as both *E. corymbosum* var. *albogilvum* Reveal (type from Indian Canyon) and *E. x duchesnense* Reveal (type from Indian Canyon); 18 (iii). The var. *viridulum* is closely allied to var. *ephedroides* standing about midway between that entity and var. *brevicaule*. There is an admitted close affinity with var. *laxifolium* westward. Some plants from near Split Mountain, Uintah County, are apparently transitional with *E. lonchophyllum* var. *saurinum* and *E. microthecum*.

***Eriogonum caespitosum* Nutt.** Mat Buckwheat. Plants perennial, matforming, mainly 1–4 dm across, the vegetative stems persistent, with branches woody and usually clothed with gray to black leaves and bases; flowering stems scapose, arising from rosette-like branches, mainly 0.5–10 cm long or lacking; leaves 2–12 mm long, 1.5–5 mm wide, spatulate to oblanceolate, elliptic or oval, tomentose, flat or essentially so, short-petiolate; inflorescence capitate, not subbtended by bracts; involucres campanulate, with the tubes 2–3.5 mm long and 3–5 mm wide, the lobes oblong, 2–3.5 mm long; flowers yellow or suffused with red, 2.5–10 mm long including the stipitate base, pilose to villous, the segments oblanceolate; achenes 3.5–5 mm long. Sagebrush, pinyon-juniper, and mountain brush communities at 1525 to 2290 m in Beaver, Box Elder, Iron, Juab, Millard, Rich, Summit, and Washington counties; Oregon to Montana, south to California, Nevada, and Colorado; 21 (iv).

***Eriogonum cernuum* Nutt.** Nodding Buckwheat. [*E. cernuum* var. *tenue* T. & G., type from Weber Valley; *E. cernuum* var. *umbraticum* Eastw., type from McElmo Creek, San Juan County]. Plants annual, becoming unbelliform, mainly 5–45 cm tall; leaves all basal or cauline up to 10 cm above the base, the blades 3–35 mm long and about as wide, ovate to oval or orbicular, tomentose on one or both sides; petioles 3–40 mm long; inflorescence glabrous, open, the branches spreading or ascending; involucres usually stalked (except in var. *vimineum*), often deflexed, obconic to campanulate, 1–2 mm long, glabrous, the 5 teeth acute; flowers white, 1–2.5 mm long, glabrous, the outer segments constricted below the middle, the margins undulate, often more or less saccate basally, the inner ones obovate; achenes 1.5–2 mm long. Shadscale, other salt desert shrub, sagebrush, pinyon-juniper, mountain brush, ponderosa pine, aspen, and spruce-fir communities at 1220 to 2810 m in Beaver, Carbon, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, Piute, Rich, Salt Lake, San Juan, Sevier, Tooele, Uintah, Utah, Washington, and Wayne counties; Canada south to California, Arizona, and New Mexico; 142 (xxvii). A phase with sessile involucres and somewhat larger flowers occurs in Millard and Beaver counties; i.e., var. *viminale* (Stokes) Reveal in Munz [*E. cernuum* ssp. *viminale* Stokes; 5 (0). A few plants from sandy sites in Kane County have inflorescences more paniculiform than usual and more uniformly short-stipitate involucres. Possibly they are of taxonomic significance.

Eriogonum clavellatum Small Comb Wash Buckwheat. Shrubs, mainly 7–20 cm tall, clump forming; leaves 3–15 mm long, 0.5–2 mm wide, narrowly oblanceolate to oblong, white-tomentose beneath, less densely so above, revolute, often with fascicled secondary ones in at least some axils; petioles very short; inflorescence cymose-umbellate, mainly 1–2.5 cm wide, glabrous; involucres on stipes mainly 1–4 mm long, glabrous, obconic to campanulate, 3.5–4.5 mm long, with

5-acutish teeth; flowers white or suffused with pink, glabrous, 3–3.5 mm long, the outer segments obovate to broadly spatulate, the inner ones narrower; achenes 3–3.5 mm long. Shadscale and blackbrush communities at ca 1325 to 1680 m in San Juan (type from Bartons range) County; endemic; 6 (i).

Eriogonum contortum **Small ex Rydb.** Grand Buckwheat. [*E. effusum* ssp. *contortum* (Small) Stokes]. Shrubs mainly 5–20 cm tall, clump-forming; leaves 5–20 mm long, 1–2 wide, linear to narrowly oblanceolate, revolute, tomentose on one or both sides; petioles very short; inflorescence cymose to cymose-umbellate, the involucres not clustered, tomentose to glabrous, involucres 1–2.5 mm long, obconic to campanulate, glabrous, the 5 teeth acutish; flowers yellow, 1.5–2.5 mm long, glabrous, the segments oblong to obovate; achenes 2–2.5 mm long. Shadscale and other salt desert shrub communities at ca 1280 to 1525 m in Grand County; Colorado; 8 (ii). This low shrub is allied to the *brevicaule* complex.

Eriogonum corymbosum **Benth.** Corymb Buckwheat. Low to tall shrubs or subshrubs, 0.7–12 dm tall, clump (seldom mat) forming; leaves 0.7–9 cm long, lanceolate to elliptic, orbicular, oblanceolate, spatulate, or linear, tomentose on one or both sides or glabrous, the margins flat to revolute; petioles 2–18 mm long; inflorescences cymose, the branches ascending to spreading or divaricate, glabrous or tomentose; involucres 1.5–4 mm long, obconic or campanulate, glabrous or tomentose, with 5 or 6 acute teeth; flower white, suffused with pink or red or yellow, 1.5–4.5 mm long, glabrous, the segments obovate to lanceolate or spatulate; achenes 2–3 mm long. This is a huge and complex species group, involving numerous morphological variants, some of which are edaphically and geographically correlated. Diagnostic criteria are few, and are often based on vegetative characteristics that form continuous clines. The species is pivotal to *E. thompsonae*, *E. lonchophyllum*, *E. leptocladon*, and *E. brevicaule*, forming hybrids with all of them. At the margins of ecological tolerance the species undergoes reduction of internode length and concurrent elongation of the inflorescence. Yellow flowers are apparently derived, at least in part, from hybridization with other species having yellow flowers (see *E. x duchesnense* under *E. brevicaule*, and both *E. thompsonae* and *E. leptocladon*). The following treatment is preliminary, but allows recognition of the more important phases of the complex. There are other forms, possibly ecotypes or incipient ecotypes, that might be worthy of recognition, but those must await more definitive work.

1. Internodes of annual growth short, the inflorescence usually much longer than the vegetative branch 2

— Internodes of annual growth elongate, the inflorescence subequal to or shorter than the vegetative branch 4

2(1). Inflorescence tomentose; plants of the Sevier River drainage, Sink Valley, and Thousand Lake Mt. .... *E. corymbosum* var. *revealianum*

— Inflorescence glabrous; plants of various distribution 3

3(2). Leaves crenately revolute; plants of the Henry Mts. .. *E. corymbosum* var. *cronquistii*

— Leaves flat or essentially so, the margins not especially crenate or revolute; plants of San Juan County .... *E. corymbosum* var. *humivagans*

4(1). Flowers yellow or pale yellow 5

— Flowers white or variously suffused with pink or red 6

5(4). Leaves glabrous on both surfaces; inflorescences glabrous; plants of southeastern Emery and eastern Wayne counties .... *E. corymbosum* var. *smithii*

— Leaves tomentose on one or both surfaces; inflorescences glabrous or tomentose; plants of different distrubution .... *E. corymbosum* var. *aureum*

6(4). Leaf blades as long as broad or nearly so; plants forming clumps mainly 6–20 dm broad; inflorescence intricately and divaricately branched; plants often of rimrock along the canyons of the Colorado River .... *E. corymbosum* var. *orbiculatum*

— Leaf blades much longer than broad; plants mainly less than 6 dm wide; inflorescence with branches not especially divaricate or sometimes so, but then of different substrates and distribution 7

7(6). Leaves mainly 3–9 cm long, more or less revolute, but not especially crenate-revolute; plants of southeastern Duchesne County .... *E. corymbosum* var. *hylophilum*

— Leaves mainly 0.5–4.5 cm long, usually crenate-revolute, less commonly flat; plants widespread .... *E. corymbosum* var. *corymbosum*

Var. *aureum* (Jones) Reveal Golden Buckwheat. [*E. aureum* var. *glutinosum* Jones; *E. fruticosum* var. *glutinosum* (Jones) A. Nels.; *E. fruticosum* A. Nels.; *E. aureum* Jones, type from near St. George; *E. crispum* L. O. Williams, type from Cedar Canyon, Iron County]. Salt and mixed desert shrub and pinyon-juniper communites at 1065 to 2565 m in Emery, Garfield, Kane, Washington, and Wayne counties; Arizona; 27 (v). It is doubtful whether the yellow-flowered material constitutes a taxon in the usual sense. The assemblage is held together by the feature of flower color alone, a character hardly viewed as reliable in some portions of the genus, and the plants are almost as variable as those of var. corymbosum, with which they are largely sympatric. Similar yellow-flowered plants from the Uinta Basin result from hybridization of *E. brevicaule* with *E. corymbosum*. Specimens from Washington County are transitional into *E. thompsonae* (see the Shivwits phase under that species).

Var. *corymbosum* [*E. corymbosum* var. *divaricatum* T. & G., type from Green River; *E. corymbosum* ssp. *divaricatum* (T. & G.) Stokes; *E. divergens* Small; *E. effusum* ssp. *corymbosum* (Benth.) Stokes; *E. effusum* var. *durum* Stokes, type from Sunnyside; *E. erectum* Reveal & Brotherson, type from west of Duchesne; *E. corymbosum* var. *velutinum* Reveal; *E. lancifolium* Reveal & Brotherson, type from east of Wellington; *E. corymbosum* var. *davidsei* type from Wellington]. Shadscale, other salt desert shrub, sagebrush, mixed desert shrub, and pinyon-juniper communities at 1400 to 2440 m, often on fine-textured or sandy soils, in Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Kane, San Juan, Sevier, Uintah, Wasatch, and Wayne counties; Colorado and Arizona; 178 (xxxv). This variety is pivotal between *E. brevicaule*, *E. lonchophyllum*, and other taxa.

Var. *cronquistii* (Reveal) Welsh comb. nov. [based on: *E. cronquistii* Reveal Madrono 19: 289. 1968]. Cronquist Buckwheat. Pinyon, holodiscus, rabbitbrush, and rockspiraea communities at ca 2680 to 2715 m in the Henry Mts., Garfield County; endemic; 3 (0). A closely similar plant is known from Thousand Lake Mt., but is tomentose throughout, except for the flowers, and is here assigned to var. *revealianum*.

Var. *humivagans* (Reveal) Welsh comb. nov. [based on: *E. humivagans* Reveal Madroño 19:291. 1968]. San Juan Buckwheat. Woody aster, rabbitbrush, and pinyon-juniper communities at 1675 to 2105 m in San Juan (type from east of Monticello) County; endemic; 3 (i).

Var. *hylophilum* (Reveal & Brotherson) Welsh comb. nov. [*E. hylophilum* Reveal Great Basin Nat. 27:190. 1968]. Gate Canyon Buckwheat. Juniper and pinyon-juniper communities at 2040 to 2535 m in Duchesne (type from Gate Canyon) County; endemic; 6 (0). Materials included within this variety are intermediate between *E. brevicaule* var. *promiscuum* and *E. corymbosum*, var. *corymbosum* especially that phase called *E. lancifolium* (q.v.). The variety is also influenced more or less by *E. brevicaule* var. *laxifolium*.

Var. *orbiculatum* (Stokes) Reveal & Brotherson Rimrock Buckwheat. [*E. effusum* ssp. *orbiculatum* Stokes]. Eriogonum, mixed desert shrub, hanging garden, and pinyon-juniper communities, often on sandstone, at 1125 to 2200 m, in Emery, Garfield, Grand, Kane, San Juan, and Wayne counties; Arizona and New Mexico; 49 (xix). Materials designated as var. *velutinum* Reveal are transitional between var. *orbiculatum* and var.

corymbosum at least in Utah specimens.

Var. *revealianum* (Welsh) Reveal Reveal Buckwheat. [*E. revealianum* Welsh, type from south of Antimony]. Sagebrush, pinyon-juniper, and bristlecone pine communities at 2135 to 2745 m in igneous gravels or clay-silts in Garfield, Kane, Piute, and Wayne counties; endemic; 13 (v). A specimen from the south end of Thousand Lake Mt. (Atwood & Thompson 7645 BRY) is like var. *cronquistii* in habit, but has broader involucres and pubescence of var. *revealianum*. Specimens from Kane County indicate a possible relationship with *E. thompsonae*.

Var. *smithii* (Reveal) Welsh comb. nov. [based on: *E. smithii* Reveal Great Basin Nat. 27: 202. 1968]. Flat Top Buckwheat. Purple-sage, matchweed, ephedra-Indian ricegrass, and rabbitbrush communties, on the Entrada Formation and on stabilized dunes, at ca 1585 to 1710 m in Emery (type from the Big Flat Top) and Wayne counties; endemic; 12 (ii). This is the most striking phase within the *corymbosum* complex. Its origin is problematical, but the possibility of hybridization cannot be discounted. Putative hybrids between var. *corymbosum* and *E. leptocladon* (q.v.) suggest such a possibility.

***Eriogonum darrovii* Hook.** Darrow Buckwheat. Annuals, mainly 3–15 cm tall, usually branched from near the base; leaves mainly cauline, the blades 4–15 mm long, 3–13 mm wide, puberulent to villous-pilose on both sides, tomentose to ovate, elliptic or orbicular; inflorescences axillary; involucres sessile, campanulate, 2–2.5 mm long, pilose, with 5 lance-ovate lobes; flowers yellow or pink, 1–2.5 mm long, hairy near the base, the outer segments broadly obovate, hooded, and conspicuously ciliate, the inner ones narrower; achenes ca 1 mm long. Pinyon-juniper community at ca 1860 m in Kane County; Arizona and Nevada; 1 (0).

***Eriogonum davidsonii* Greene.** Davidson Buckwheat. [*E. baileyi* var. *davidsonii* (Greene) Jones; *E. mosestum* var. *davidsonii* (Greene) Jepson; *E. juncinellum* Gand.; *E. vimineum* ssp. *juncinellum* (Gand.) Stokes]. Annuals, 6–40 cm tall; leaves all basal (rarely some above the base), the blades 6–20 mm long and as wide or wider, orbicular, white tomentose beneath and above or glabrate above; petioles 3–20 mm long; inflorescences glabrous, the branches erect-ascending; involucres sessile or terminal, narrowly obconic, 2.5–5 mm long, glabrous, the 5 teeth acutish; flowers white to pink, 1.5–2 mm long, glabrous, the segments obovate to oblong; achenes ca 2 mm long. Creosote bush, Joshua tree, mixed warm desert shrub, and pinyon-juniper communities at 795 to 1680 m in Kane and Washington counties; California, Nevada, Arizona, and Mexico; 7 (0).

***Eriogonum deflexum* Torr. in Ives** Skeletonweed Buckwheat. [*E. deflexum* var. *nevadense* Reveal]. Annuals, 5–40 (50) cm tall; leaves all basal; blades 6–30 (40) mm long and as wide or wider, orbicular to subreniform, rounded to cordate basally, tomentose on one or both sides; petioles 0.3–7 cm long; inflorescences usually spreading and umbrellalike, glabrous; involucres stipitate to subsessile or sessile, glabrous, deflexed, obconic to somewhat campanulate, mainly 1.5–2 mm long, the 5 teeth acutish; flowers white, sometimes pinkish, 1–2 mm long, glabrous, the outer segments cordate, the inner ones narrower; achenes 1.5–2 mm long. Creosote bush, Joshua tree, blackbrush, other warm desert shrub, shadscale, and juniper communities at 760 to 1985 m in Garfield, Juab, Kane, Millard, San Juan, Washington, and Wayne counties; Nevada, Arizona, California, and Mexico; 39 (xiii). This species is a close ally of *E. hookeri*, *E. brachypodium*, and *E. insigne*, all of which have been included previously within an expanded *E. deflexum*. Some specimens from Washington County have strict branches like *E. insigne*, but are otherwise *E. deflexum*. I follow recent tradition in treating the taxa as separate species. The var. *nevadense*, in Utah at least, lacks both geographical and morphological continuity. Our material belongs to **var. *deflexum*.**

***Eriogonum divaricatum* Hook.** Spreading Buckwheat. Annuals, prostrate to decumbent-ascending, the stems 5–22 cm long, dichotomously branched; leaves cauline and basal, the blades 3–30 mm long, 3–20 mm wide, oval to orbicular, puberulent with crinkly hairs; involucres sessile, borne in axils of bracteate leaves on spreading-decurved branches, obconic, 1–2 mm long, pilose, 5-lobed; flowers yellowish or suffused with red, 1–2 mm long, puberulent and glandular, the segments oblong to lanceolate; achenes 1.5–2 mm long. Shadscale, mixed desert shrub, and pinyon-juniper communities at 1155 to 2015 m in Emery, Garfield, Millard, San Juan, Uintah, and Wayne counties; Wyoming, Colorado, New Mexico, and Arizona; 12 (i).

Eriogonum fasciculatum **Benth.** Mojave Buckwheat. Shrubs, mainly 2–8 dm tall, clump-forming; leaves cauline, often with some fascicled ones in lower axils, 4–18 mm long, 1–5 mm wide, usually more or less revolute, linear to narrowly oblong or oblanceolate, more or less tomentose on one or both sides; inflorescences long-peduncled, divarcately branched or subcapitate, tomentulose; involucres obconic to campanulate, 2–3.5 mm long, the 5 obtusish lobes with hyaline margins; flowers white to pink, 2–3 mm long, villous-pilose, the segments obovate; achenes 2–2.5 mm long. Warm desert shrub communities at 730 to 1495 m in Washington County; Nevada, California, Arizona, and Mexico; 25 (i). Our material has been assigned to var. ***polifolium*** **(Benth.) T. & G.** [*E. polifolium* Benth. in DC.]. A specimen with provenience of Emery County (Cottam 5224A BRY) is extant, but might be mislabeled.

Eriogonum flexum **Jones.** Bent Buckwheat. [*E. flexum* var. *ferronis* Jones, type from near Ferron; *Stenogonum flexum* (Jones) Reveal & Howell]. Annuals, 4–35 cm tall; leaves all basal (rarely some whorled at nodes of inflorescence); blades 3–28 mm long and about as wide, orbicular to oval, truncate to subcordate basally, puberulent to glabrous and sometimes glandular on one or both surfaces; petioles 3–40 mm long; involucres stipitate, the filiform stipes commonly abruptly bent below the involucre and often glandular below, campanulate, in 2 whorls, each 3-lobed; flowers yellow, 1.5–4 mm long, puberulent, the segments lanceolate; achenes 2–2.5 mm long. Shadscale, mat-saltbush, blackbrush, and pinyon-juniper communities, often on fine-textured substrates, at 1430 to 1865 m in Carbon, Emery, Garfield, Kane, San Juan, Uintah, and Wayne counties; Colorado and Arizona; 34 (iii). Although regarded by some workers as belonging, with *E. salsuginosum*, in the segregate genus *Stenogonum* because of their peculiar involucres, both species appear to be more nearly allied to species within *Eriogonum* proper than they are to each other (see *E. inflatum*).

Eriogonum gordonii **Benth. in DC.** Gordon Buckwheat. Annuals, mainly 8–60 cm tall; leaves all basal; blades 9–55 mm long, oval to suborbicular, obtuse to truncate or cordate basally, green above, paler beneath, softly spreading-hairy; petioles 0.5–10 cm long or more; inflorescences spreading-ascending, glabrous or hairy; involucres on stipes mainly 3–20 mm long, obconic-campanulate, 0.6–1.3 mm long, glabrous, with 5 obtusish teeth; flowers white, 1–2.5 mm long, glabrous, the segments obovate to oblong or oblanceolate; achenes 1.8–2.5 mm long. Salt desert shrub, shadscale, and juniper or pinyon-juniper communities, on fine-textured saline soils, at 1110 to 2015 m in Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Kane, and Uintah counties; Wyoming to Nebraska, south to Arizona, and New Mexico; 49 (vi).

Eriogonum heermannii **Dur. & Hilg.** Heermann Buckwheat. Shrubs, mainly 1–6 dm tall, clump forming, with intricately and divaricately branched inflorescences appearing cushionlike; leaves mainly 3–17 mm long, 2–5 mm wide, the blades elliptic to spatulate, tomentose on one or both sides, more or less revolute; petioles 3–10 mm long; inflorescence cymose, the branches angled or ribbed and sulcate between the ribs; involucres sessile, glabrous, campanulate, 0.6–1.5 mm long, with 5 rounded teeth; flowers white (yellowish?), 1.5–3 mm long, glabrous, the outer segments obovate, the inner ones narrower; achenes 2–2.5 mm long. Blackbrush, mixed desert shrub, mountain brush, and pinyon-juniper communities (often on rock outcrops) at ca 1220 to 2135 m in Washington County; Nevada, Arizona, and California; 10 (ii). All material from Utah examined by me belongs to var. ***sulcatum*** **(Wats.) Munz & Reveal** [*E. sulcatum* Wats., type from near St. George]. The var. ***subracemosum*** **(Stokes) Reveal** [*E. howellii* var. *subracemosum* Stokes] is present in the region also. It differs in having stems less angled and involucres more racemosely arranged.

Eriogonum heracleoides **Nutt.** Whorled Buckwheat. [*E. heracleoides* var. *utahense* Gandg., type from Cache County]. Perennial, mat-forming, mainly 2–6 dm across; vegetative stems persistent, the branches woody and more or less clothed with persistent, gray to brown or blackish leaves and bases; flowering stems with whorled leaves near the middle, arising from rosettelike bases, mainly 1.5–5 dm tall; leaves 2–7 cm long, 3–15 mm wide, the blades elliptic to oblong or oblanceolate, tomentose on one or both sides, entire, flat or essentially so; petioles 3–30 mm long; inflorescences umbellate or twice umbellate, rarely capitate, tomentose; involucres sessile or on stipes to 40 mm long, obconic to campanulate, 4–10 cm long, the lobes subequal to the tube or longer; flowers white or cream (or yellow), 4–9 mm long, including the stipitate base, the segments spatulate to elliptic or oblong; achenes 2–5 mm long. Sagebrush, mountain brush, juniper, pinyon-juniper, Douglas fir, and aspen communities at 1310 to 3050 m in Box Elder, Cache, Daggett, Davis, Duchesne, Juab, Millard, Cache, Salt Lake, Sanpete, Summit, Tooele, Uintah, Utah, and Wasatch counties; Canada, south to California, Nevada, and Wyoming; 83 (ii). This plant forms putative hybrids with phases of *E. umbellatum*. A specimen with features of *E. heracleoides* but with yellow flowers (Neese 14148 BRY) might indicate hybridization.

Eriogonum hookeri **Wats.** Watson Buckwheat. [*E. deflexum* ssp. *hookeri* (Wats.) Stokes; *E. deflexum* ssp. *hookeri* var. *gilvum* Stokes, type from American Fork Canyon]. Annuals, mainly 8–60 mm tall; leaves all basal; blades mainly 10–50 mm long and as broad or broader, orbicular to reniform, tomentose on both sides, obtuse to cordate basally, flat to undulate; inflorescences glabrous, umbrellalike; involucres sessile, deflexed, campanulate to hemispheric, 1–2 mm long, glabrous; flowers yellow, soon suffused with pink to dark red, 1.5–2.7 mm long, glabrous, the outer segments cordate, the inner ones narrower; achenes 2–2.5 mm long. Mixed desert shrub, sagebrush, pinyon-juniper, aspen, and spruce-fir communities at 1135 to 3050 m in Beaver, Box Elder, Carbon, Duchesne, Emery, Garfield, Iron, Juab, Millard, Piute, San Juan, Sevier, Tooele, Uintah, Utah (type from American Fork Canyon), and Wayne counties; Wyoming, Colorado, Arizona, Nevada, and California; 70 (xviii).

Eriogonum howellianum **Reveal** Howell Buckwheat. Annual, 5–30 cm tall, simple or branched from the base; leaves all basal; blades 6–25 (30) mm long and about as wide, oval to suborbicular, pubescent with long, soft, spreading hairs on at least the lower surface, obtuse to subcordate basally; petioles 3–40 mm long; inflorescences divaricately branched, the branches with scattered, stipitate, dark glands; involucres with filiform stipes 3–20 mm long or more, obconic to campanulate, glabrous, 1.3–2 mm long, usually 5-toothed; flowers yellowish or reddish, 1–2 mm long, the segments lanceolate, mostly obscured by spreading-villous hairs; achenes 1.5–2 mm long. Desert shrub, desert almond, and shadscale communities at 1460 to 1740 m in Juab, Millard (type from SE of Garrison), and Tooele counties; Nevada; a Great Basin endemic; 8 (i). This taxon is allied to *E. inflatum* and *E. flexum*.

Eriogonum inflatum **T. & G.** Bottlebush; Bottlestopper; Desert trumpet. Annual or perennial herbs, mainly 8–100 cm tall; leaves all basal; blades 4–30 mm long and about as wide or wider, orbicular to oblong or reniform, hirtellous on one or both sides, obtuse to cordate basally, entire to undulate-crisped; petioles 0.5–6 cm long; peduncles and usually the primary and secondary rays of inflorescence inflated, rarely not; inflorescence umbellate-cymose; involucres borne on glabrous, capillary to filiform stipes 5–45 mm long or more, obconic, 0.7–1.5 mm long, glabrous, the 5 lobes acutish; flowers yellow or reddish, 1–2.5 mm long, densely strigose, the segments lanceolate to ovate; achenes 2–2.5 mm long. Warm desert shrub, mixed desert shrub, salt desert shrub, and pinyon-juniper communities at 760 to 1955 m in Carbon, Duchesne, Emery, Garfield, Grand, Kane, San Juan, Uintah, Washington, and Wayne counties; California, Nevada, Colorado, Arizona, New Mexico, and Mexico; 90 (xvii). Annuals within this species have been regarded as var. ***fusiforme*** (Small) Reveal [*E. fusiforme* Small], and perennials as var. ***inflatum***. The former occurs at the margins of the range of the latter, but is also sympatric.

The segregation appears to be moot, owing to the flowering of specimens of both phases during the initial year.

Eriogonum insigne Wats. Unique Buckwheat. [*E. deflexum* var. *insigne* (Wats.) Jones; *E. deflexum* ssp. *insigne* (Wats.) Stokes; *E. exaltatum* Jones; *E. deflexum* ssp. *exaltatum* (Jones) Stokes]. Annuals, mainly 8–100 cm tall; leaves all basal; blades 8–50 mm long (or more) and as wide or wider, orbicular to reniform, obtuse to cordate basally, tomentose on one or both sides; petioles 0.6–10 cm long; peduncles simple or branched from the base, inflorescences open cymose, the branches glabrous, erect to spreading; involucres sessile or with stipes to 6 mm long, obconic to campanulate, 2–3 mm long, glabrous, the 5 teeth obtusish; flowers white or suffused with pink, 1.5–2 mm long, glabrous, the outer segments cordate to oblong-cordate, the inner ones narrower; achenes 2–2.5 mm long. Creosote bush, other warm desert shrub, and mixed desert shrub communities at 730 to 1170 m in Iron (type from Red Creek) and Washington counties; California, Nevada, and Arizona; 6 (0).

***Eriogonum jamesii* Benth. in DC.** James Buckwheat. Matforming perennials, mainly 1–6 dm wide; vegetative stems persistent, the branches woody, usually clothed with persistent, ashy to dark brown leaf bases; flowering stems subscapose, arising from rosettelike branches, mainly 6–30 cm long; leaves 1–9 cm long, 4–20 mm wide, the blades elliptic to obovate or ovate, tomentose on one or both sides, entire or undulate, flat or essentially so; petioles 0.5–6 cm long; inflorescences capitate or once or twice umbellate, tomentose, with foliose bracts at the nodes; involucres sessile, campanulate, 3–14 mm long, tomentose, the 5–8 teeth obtusish, erect to spreading; flowers yellow, 4–11 mm long, including the stipitate base, the segments spatulate to obovate; achenes 4–5 mm long. Sagebrush, mountain brush, pinyon-juniper, and ponderosa pine communities at 1585 to 2685 m in Carbon, Duchesne, Emery, Kane, San Juan, Sevier, Washington, and Wayne counties; Wyoming to Kansas, south to Arizona, New Mexico, Texas, and Mexico; 40 (viii). This is a remarkably beautiful species, with its bright sulphur-yellow flowers. The species varies from population to population, and specimens from Utah have been regarded as belonging to two varieties, although more segregation seems possible. Dwarf plants from Washington and adjacent Kane counties have pilose hairs over the tomentum on the upper leaf surfaces; they belong to **var. *rupicola* Reveal** (type from Zion National Park). The remainder of the Utah specimens are included within **var. *flavescens* Wats.**, but that taxon consists of variants of about equal value to var. *rupicola*. Specimens from San Juan County have capitate inflorescences, and material from western Emery County has huge involucres.

***Eriogonum leptocladon* T. & G.** Sand Buckwheat. Shrubs, mainly 2–10 dm tall or more, clump forming; leaves often deciduous at anthesis, mainly 10–45 mm long, 2–10 mm wide, linear to narrowly lanceolate or oblanceolate, more or less revolute to flat, tomentose on one or both sides; petioles 1–6 mm long; inflorescences tomentose or glabrous, much longer than the vegetative stems; involucres cymose-racemose, sessile or nearly so, obconic to campanulate, 1.5–3 mm long, glabrous or tomentose, the 5 teeth acute to rounded; flowers yellow, yellowish, or white and often suffused with pink, 2–3.5 mm long, glabrous, the segments obovate; achenes 2.5–3.5 mm long. Three rather weak varieties are present.

1. Flowers yellow; plants of the central Canyonlands vicinity .... *E. leptocladon* var. *leptocladon*
— Flowers white; plants sometimes distributed as above, or otherwise 2
2(1). Branches of inflorescence yellowish green, glabrous or rarely tomentose; plants of Garfield and Kane counties .... *E. leptocladon* var. *papiliunculum*
— Branches of inflorescence green to gray-green, tomentose or glabrous; plants of broad or other distribution .... *E. leptocladon* var. *ramosissimum*

Var. *leptocladon* [*E. microthecum* var. *leptocladon* (T. & G.) T. & G.; *E. effusum* ssp. *leptocladon* (T. & G.) Stokes; *E. effusum* ssp. *pallidum* var. *shandsii* Stokes, type from Indian Creek, San Juan County]. Purple-sage, ephedra, sand sagebrush, blackbrush, saltbush, and pinyon-juniper communities, usually in sand or on stabilized dunes, at 1340 to 1895 m in Emery, Garfield, Grand (type from Green River), San Juan, Sevier, and Wayne counties; endemic; 39 (x). This phase forms putative hybrids with *E. corymbosum* var. *corymbosum* (Neese 6829 -6833 BRY). The apparent backcrosses to *corymbosum* have broad leaves and yellowish flowers or are broad leaved and have white or pinkish flowers. The latter plants simulate var. *ramosissimum* and suggest at least one possible origin for that entity.

Var. *papiliunculum* **Reveal** Little-butterfly Buckwheat. Ephedra-vanclevea, sand sagebrush, other sand desert shrub, and juniper communities at 1400 to 1830 m in Garfield, Kane, San Juan, and Wayne counties; Arizona (?); 10 (ii). These plants have broader leaves than in var. *leptocladon* and yellowish green inflorescences. They are intermediate in most respects between var. *ramosissimum* and *E. corymbosum* with possibly both vars. *corymbosum* and var. *aureum* as contributors. Specimens transitional to both var. *ramosissimum* and *E. corymbosum* var. *aureum* are known.

Var. *ramosissimum* (Eastw.) Reveal Eastwood Buckwheat. [*E. ramosissimum* Eastw., type from near Butler Wash, San Juan County]. Vanclevea, yucca, purple-sage, sand sagebrush, blackbrush, and juniper communities at 1310 to 1770 m in Garfield, Kane, San Juan, and Wayne counties; Arizona, Colorado, and New Mexico; 14 (ii). This plant appears to be closely allied to *E. wrightii*, q.v.

***Eriogonum lonchophyllum* T. & G.** Longleaf Buckwheat. Subshrubs or shrubs, mainly 8–80 cm tall; vegetative branches with leaves all at base of current growth or with leaves separated by elongated internodes; leaves mainly 2–11 cm long, 2–12 mm wide, linear to elliptic, lanceolate, or oblanceolate, tomentose on one or both sides, margins entire to crenate, plane to revolute; petioles 3–20 mm long; peduncles and inflorescences glabrous or tomentose, cymose-corymbose to cymose-capitate; involucres usually sessile, obconic to campanulate, 2–4 mm long, glabrous, 5-lobed; flowers white, cream, or suffused with pink, 2–4 mm long, glabrous, the segments subequal; achenes 2.5–3.5 mm long. As is typical of other species complexes in the perennial versus shrubby species in *Eriogonum*, the *E. lonchophyllum* phases demonstrate genetic compatibility with members of other complexes. And, these likewise tend to precipitate out more or less uniform phases on distinctive soils or geologic substrates. Problems of interpretation of the distinctive groupings, their origins, and relationships are not made easier by the linear system of classification and nomenclature usual in plant taxonomy. Instead of taxa (both ecotypes and microspecies) being related by descent from a common ancestor, they might have resulted from a reticulate relationship involving two or more parental taxa. There are two more or less distinctive taxa in Utah that fall within the circumscription of *E. lonchophyllum*, as described above. In species of genera in other families these would be regarded as belonging to the same taxon, in a broad sense, but here they might have had separate origins. The following treatment is, therefore, tentative.

1. Plants acaulescent or essentially so, the internodes of vegetative stems very short; growing on ridge crests along the Tavaputs divide and elsewhere .... *E. lonchophyllum* var. *lonchophyllum*

— Plants definitely caulescent, the internodes of vegetative stems readily apparent; growing on Mowry Shale and closely adjacent strata in northern Uintah County .... *E. lonchophyllum* var. *saurinum*

Var. *lonchophyllum* [*E. intermontanum* Reveal, type from the Roan Cliffs, Grand County]. Sagebrush, mountain brush, and Douglas fir communities, mainly on Green River and other calcareous formations] at 2285 to 2745 m in Emery, Grand, and Uintah counties; Colorado and New Mexico; 11 (ii). This variety forms intermediates with *E. corymbosum* downslope in Uintah County (the Rainbow phase); 21 (0). The apparent hybrids are transitional from one extreme to the other, with individuals simulating not only var. *saurinum* but also the *E. lancifolium* and *E. corymbosum* var. *davidsei* phases o *E. corymbosum* var. *corymbosum* (q.v.). The similarity of this taxon to both *E. batemanii* var. *batemanii* and *E. spathulatum* is great. It is likewise similar to *E. brevicaule* through the var. *promiscuum*.

Var. *saurinum* (Reveal) Welsh comb. nov. [based on: *E. saurinum* Reveal Great Basin Nat. 27: 196. 1968]. Dinosaur Buckwheat. Eriogonum, juniper, serviceberry, pinyon-juniper, and ponderosa pine, mainly on Wasatch, Mowry, Curtis, Entrada, Carmel, and Moenkopi formations, at 1585 to 1895 m in northern Uintah (type from 10 mi E of Vernal) County; endemic; 33 (vi). Much of var. *saurinum* grows on the siliceous, acidic Mowry Shale Formation. That material, though variable, is the most uniform phase of the variety. Evidence exists that even the Mowry Shale phase is partially, at least, a product of introgression with *E. corymbosum*. On other formations adjacent to the Mowry Shale the plants vary from the type; e.g., in the Steinaker Reservoir area (Curtis, Entrada, and Carmel formations) the inflorescences are suggestive of those of *E. brevicaule* var. *viridulum* on the one hand and *E. microthecum* on the other; in the Asphalt Ridge (Wasatch Formation) vicinity the plants bear features of *E. corymbosum* and, in the Bourdette Draw vicinity (Moenkopi Formation), south of Blue Mountain, the plants again share features of *E. brevicaule*, in a broad sense. Though trends exist that indicate direct relationship with *E. lonchophyllum*, this variety might represent mainly recombinants of various *E. brevicaule* and *E. corymbosum* introgressants. More work is indicated.

***Eriogonum maculatum* Heller** Spotted Buckwheat. [*E. angulosum* var. *maculatum* (Heller) Jepson; *E. angulosum* ssp. *maculatum* (Heller) Stokes]. Annuals, mainly 8–37 cm tall or more; leaves basal and cauline (foliose bracteate); basal leaf blades 5–25 mm long, 3–15 mm wide, oval to obovate or elliptic, tomentose on one or both sides; petioles 3–15 mm long; bracteate leaves reduced and becoming sessile upward; inflorescences tri- or dichotomous, tomentose; involucres on filiform stipes 5–30 mm long or more, broadly campanulate, 1–2.5 mm long, glandular-puberulent, with 5 broad teeth; flowers white to yellowish or pink, 1.5–2.8 mm long, glandular-puberulent, the outer segments ovate and cupulate, shorter than the slender inner ones; achenes 1–1.5 mm long. Creosote bush, Joshua tree, blackbrush, pinyon-juniper, live oak, and mixed desert shrub communities, at 730 to 1830 m in Box Elder, Juab, Millard, Tooele, and Washington counties; Washington and Idaho, south to California, Nevada, and Arizona; 25 (iv).

***Eriogonum microthecum* Nutt.** Slender Buckwheat. Shrubs, mainly 4–100 cm tall, clump forming; leaves 4–35 mm long, 1–7 mm wide, elliptic to linear or oblanceolate, tomentose on one or both sides, the margins flat or revolute; petioles 1–5 mm long; inflorescences cymose, the branches ascending to spreading, glabrous or tomentose; involucres sessile to short-stipitate, obconic, 1–3.5 mm long, tomentose or glabrous, with 5 obtusish to rounded teeth; flowers white or suffused with pink, 2–3.2 mm long, glabrous, the segments obovate; achenes 2–3 mm long. Salt desert shrub, mixed desert shrub, sagebrush, pinyon-juniper, pondorosa pine, mountain brush, and white fir communities at 1125 to 2900 m in all Utah Counties (except Sanpete, Duchesne, Wasatch, Salt Lake, Davis, Weber, and Morgan); Washington to Montana, south to California, Nevada, Arizona, and New Mexico; 166 (xxxvi). There are two intergrading phases of this species in Utah, distinguished only by leaves being flat or revolute. The former have been designated as **var. *laxiflorum* Hook.** [*E. tenellum* var. *grandiflorum* Gand, type from Utah], and the latter as **var. *foliosum* (T. & G.) Reveal** [*E. effusum* var. *foliosum* T. & G.; *E. simpsonii* Benth. in DC.; *E. friscanum* Jones, type from Frisco; *E. nelsonii* L. O. Williams, type from Geyser Basin, San Juan County]. Specimens that are intermediate between *E. microthecum* and *E. brevicaule* are known (Neese 14531 a — c BRY), and likewise with *E. lonchophyllum* var. *saurinum* (Neese 8495 BRY). Despite its tendency to form intermediates with other taxa, the slender buckwheat is not known to hybridize with *E. corymbosum*, with which it is typically contrasted in keys. A report of *E. leptophyllum* (Torr.) Woot. & Standl. belongs here.

Eriogonum nidularium **Cov.** Birdnest Buckwheat. Annuals, mainly 5–20 cm tall, usually with erect-ascending branches from near the base; leaves all basal, 3–20 mm long and as wide, orbicular, tomentose on one or both sides; petioles 4–30 mm long; inflorescences densely branched, tomentose; involucres sessile, obconic, 0.6–1 mm long, appressed-erect, 5-toothed; flowers yellowish or reddish, 1.5–3 mm long, glabrous, the outer segments broadly obovate to flabellate, the inner ones narrower; achenes ca 1 mm long. Mixed desert shrub at ca 1065 to 1220 m in Washington County; Oregon to Idaho, south to California and Arizona; 3 (0).

Eriogonum nummulare **Jones** Coin Buckwheat. Shrubs or subshrubs, sprawling to erect, mainly 1–8 dm tall, clump forming; leaves 4–30 mm long, 4–17 mm wide, orbicular to elliptic, lanceolate, or obovate, tomentose on both surfaces, plane or undulare; petioles 1–15 mm long; inflorescences cymose or cymose-racemose, tomentose or glabrous, the branches erect-ascending or spreading; involucres sessile or on stipes 1–2 mm long, obconic, 1.5–3.5 mm long, tomentose or glabrous, 5-toothed; flowers white or suffused with pink, 1.5–3 mm long, the segments obovate to oblong; achenes 1.5–3.5 mm long. Two varieties occur in Utah.

1. Inflorescences glabrous; involucres narrowly obconic, glabrous; plants uncommon .... *E. nummulare* var. *ammophilum*
— Inflorescences tomentose; involucres broadly obconic, tomentose; plants locally common .... *E. nummulare* var. *nummulare*

Var. *ammophilum* (Reveal) Welsh comb. nov. [based on: *E. ammophilum* Reveal Phytologia 23: 163. 1972]. Ibex Buckwheat. Shadscale, horsebrush, winterfat, rabbitbrush, ephedra, and pinyon-juniper communities at 1460 to 1830 m in Millard (type from Ibex Warm Point) County; endemic; 8 (v). These plants are intermediate between *E. nummulare*, in a strict sense, and *E. batemanii* var. *eremicum*. They share the caulescent habit of the former with the glabrous inflorescences and involucres of the latter. The distribution is intermediate between the two.

Var. *nummulare* [*E. kearneyi* Tidestr., type from W of Tooele; *E. dudleyanum* Stokes, type from Skull Valley]. Fourwing saltbush, rabbitbrush, sagebrush, salt desert shrub, and juniper communities at 1095 to 1985 m in Juab, Kane, Millard, Tooele (type from Dutch Mountain), and Washington counties; California, Nevada, and Arizona; 30 (v). Specimens from sandy areas of eastern Tooele County (the *kearneyi* phase) south to Kane and Washington counties have leaves proportionally longer than broad, but the variation is continuous westward with more typical material.

Eriogonum nutans **T. & G.** Dugway Buckwheat. [*E. deflexum* ssp. *ultrum* Stokes, type from Sevier Valley; *E. rubiflorum* Jones, type from Dugway, Tooele County]. Annuals, mainly 5–30 cm tall; leaves all basal; blades 5–25 mm long and as wide or wider, orbicular to reniform, obtuse to cordate basally, tomentose on one or both sides; petioles 5–28 mm long; inflorescences more or less trichotomously branched, glabrous or more or less stipitate-glandular; involucres with slender stipes mainly 3–12 mm long, finally decurved, broadly campanulate, 2–3 mm long, more or less glandular, the 5 teeth with hyaline margins; flowers white or suffused with pink or red, glabrous, 2–3 mm long, the outer segments oblong-obovate, the inner ones narrower; achenes 1.5–2 mm long. Shadscale and sagebrush communities at ca 1525 to 1830 m in Beaver, Carbon, Sevier, and Tooele counties; Oregon and Nevada; 3 (i).

Eriogonum ovalifolium **Nutt.** Cushion Buckwheat. Pulvinate-caespitose, often mound-forming perennials, mainly 0.5–4 dm across; vegetative branches clothed with persistent, ashy to black leaf bases, terminated by rosettes of leaves; fertile stems scapose, 1–30 cm tall; leaf blades 2–6 cm long, 1–15 mm wide, tomentose on both surfaces, orbicular to elliptic, oblanceolate, or spatulate; petioles 1–50 mm long or more; inflorescences capitate, tomentose; involucres solitary or few to several, obconic to campanulate, 2–5.6 mm long, tomentose, with 5 teeth; flowers white, cream, yellow, or suffused with pink, red, or purple, 3–7 mm long, glabrous, the outer segments oval to orbicular, the inner ones narrower; achenes 2–3 mm long. Shadscale, bullgrass, winterfat, Grayia, sagebrush, pinyon-juniper, fringed sagebrush, and alpine meadow communities at 1370 to 3420 m in Beaver, Box Elder, Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, Salt Lake, San Juan, Sanpete, Sevier, Tooele, Uintah, Utah, Washington, Wayne, and Weber counties; Canada, south to California, Arizona, and New Mexico; 202 (xxv). This species has been treated as having three varieties in Utah; var. *ovalifolium* [*E. ovalifolium* var. *utahense* Gandg., type from Cache County?], with white or whitish flowers that ultimately turn pink, red, or purple; var. *multiscapum* Gandg., with yellow flowers; and var. *nivale* (Canby) Jones [*E. nivale* Canby], a dwarf, small-flowered plant of high elevations. The segregation has not proved to be more than arbitrary, with diagnostic features segregating specimens, not taxa.

Eriogonum palmerianum **Reveal in Munz** Palmer Buckwheat. [*E. plumatella* var. *palmeri* T. & G.; *E. baileyi* var. *tomentosum* Wats.]. Annuals, mainly 6–25 (30) cm tall; leaves all basal; blades 4–23 mm long and as wide or wider, orbicular to subreniform, obtuse to cordate basally, tomentose on one or both sides; petioles 3–40 mm long; inflorescences branched from near the base, tomentose, the branches often divaricate; involucres sessile, appressed, obconic, 1.2–2 mm long, tomentose, with 5 acute teeth; flowers white or pink, 1.5–2.4 mm long, glabrous, the outer segments broadly oblanceolate or obovate, the inner ones narrower; achenes 1.5–2 mm long. Blackbrush, shadscale, cheatgrass, rabbitbrush, desert almond, sagebrush, and pinyon-juniper communities at 1155 to 1985 m in Beaver, Box Elder, Garfield, Grand, Kane, Millard, San Juan, Sevier, Tooele, and Washington counties; Nevada to Colorado, California, Arizona, and New Mexico; 44 (x).

Eriogonum panguicense **(Jones) Reveal** Panguitch Buckwheat. [*E. pauciflorum* var. *panguicense* Jones, type from Panguitch; *E. spathulatum* var. *panguicense* (Jones) Stokes; *E. chrysocephalum* var. *alpestre* Stokes, type from Cedar Breaks; *E. panguicense* var. *alpestre* (Stokes) Reveal]. Pulvinate to caespitose perennial herbs, mainly 5–20 cm across; vegetative stems abbreviated, more or less clothed with ashy to black leaf bases and terminated by clustered leaves; flowering stems scapose, 2–30 cm long, glabrous; leaves 4–70 mm long, 2–8 (10) mm wide, linear to elliptic, oblanceolate, lanceolate, ovate, or obovate, obtuse to cuneate basally, plane or somewhat revolute; petioles 1–12 mm long; inflorescences glabrous, capitate or rarely branched; involucres sessile, several, obconic to campanulate, 2–3.7 mm long, the 5 teeth acute to obtuse; flowers white, often suffused with red, 2–3 mm long, glabrous, the segments oblong to lance-oblong; achenes 3--4 mm long. Pinyon-juniper, sagebrush, ponderosa pine, pygmy sagebrush, bristlecone pine, and spruce-fir communities, usually on limestone, at 1675 to 3355 m in Garfield, Iron, Kane, Sevier, and Washington counties; endemic; 48 (xi). This attractive buckwheat is closely allied to both *E. batemanii* and *E. spathulatum*, with whom it is partially sympatric. The species differs from both, however, in the usually unbranched inflorescences and smaller stature. It consists of a series of more or less disjunct populations growing on peculiar calcareous strata. Each population differs in subtle ways from all others, and, if one is chosen for varietal status, the remainder require similar recognition. The overall status, as a mosiac of variation, seems to dictate against recognition of infraspecific categories.

Eriogonum pharnaceoides **Torr. in Sitgr.** Wirestem Buckwheat. Annuals, mainly 6–30 cm long; leaves basal and cauline (foliose bracteate); blades 8–35 mm long, 1–6.5 mm wide, linear to narrowly oblanceolate, tomentose on one or both sides; petioles 1–5 mm long or lacking; inflorescences cymose, tomentulose; involucres on filiform stipes mostly 8–50 mm long, these often curved, campanulate, usually pilose, 3–4 mm long, with 5 oblong teeth; flowers yellow, 2–3 mm long, glabrous, the outer segments cordate and more or less cupulate, the inner ones narrower and surpassing the outer; achenes 1.5–2 mm long. Pinyon-juniper and ponderosa pine communities at ca 1830 to 2640 m in Iron and Washington counties; Nevada, Arizona, and New Mexico; 5 (0). Our material belongs to var. ***cervinum*** Reveal (type from Pine Valley Mts.).

Eriogonum polycladon **Benth. in DC.** Leafy Buckwheat. [*E. vimineum* ssp. *polycladon* (Benth.) Stokes]. Annuals, mainly 15–60 cm tall, the leafy stems erect; leaves basal and cauline; blades 6–18 mm long, 4–13 mm wide, obovate to elliptic, ovate, or suborbicular, tomentose on one or both sides; petioles 2–15 mm long; inflorescences tomentose, the branches erect-ascending; involucres sessile, appressed-erect, 1.5–2.5 mm long, glabrous or tomentose, with 5 obtuse teeth; flowers white or suffused with pink, 1.5–2.5 mm long, glabrous, the outer segments broadly obovate, the inner somewhat narrower; achenes 1–1.5 mm long. Sagebrush and pinyon-juniper communities at ca 1675 to 1830 m in Kane and Washington counties; Arizona, New Mexico, Texas, and Mexico; 6 (ii).

Eriogonum puberulum **Wats.** Red Creek Buckwheat. Annuals, mainly 4–30 cm tall; leaves basal and cauline (leafy bracteate); blades 2–15 mm long and about as wide, obovate to orbicular, puberulent to pilosulose on one or both sides; petioles 1–1.5 mm long; inflorescences puberulent, more or less dichotomously branched; involucres obconic, 0.6–1.5 mm long, mainly obscured by cupulate, long-lobed, nodal bracts, with 5 obtuse lobes; flowers white or suffused with red, 1.5–2.2 mm long, glabrous or scabrous, the segments oblong, sometimes somewhat cordate basally; achenes ca 1 mm long. Blackbrush, pinyon-juniper, mountain brush, and ponderosa pine communities at 1050 to 2745 m in Beaver, Iron (type from Red Creek), Millard, and Washington counties; Nevada; 7 (0).

Eriogonum pusillum **T. & G.** Slender Buckwheat. [*E. reniforme* ssp. *pusillum* (T. & G.) Stokes]. Annuals, 5–30 cm tall; leaves all basal; blades 3–20 mm long and about as wide, obovate to oval, tomentose on one or both sides; petioles 6–30 mm long; inflorescences more or less trichotomous, glabrous or the bracts glandular; involucres on slender, glabrous stipes 3–40 mm long, campanulate, 1–1.7 mm long, glandular-puberulent, the 5 lobes acute to obtuse; flowers yellow, 2–2.5 mm long, glandular-scaberulous, the segments oblong; achenes ca 1 mm long. Creosote bush and Joshua tree communities at ca 760 m in Washington County; Oregon and Idaho, south to California and Arizona; 1 (i).

Eriogonum racemosum **Nutt.** Redroot Buckwheat. Perennial, scapose or subscapose herbs, 16–100 cm tall, from a simple or branched caudex; leaves all basal or some foliose-bracteate ones at nodes of inflorescence; blades 10–100 mm long, 6–38 mm wide, elliptic, oblong, oval, or ovate, tomentose on one or both sides, obtuse to truncate or cordate basally; petioles 6–100 mm long or more; inflorescences often swollen below the nodes, simple or branched, the branches erect-ascending, tomentose or glabrous; involucres sessile, racemosely arranged, obconic to campanulate, 2–6 mm long, tomentose or glabrous, with 5 acute teeth; flowers white or suffused with pink, rose, or scarlet, 2.5–5.5 mm long, glabrous, the segments oblong or oblanceolate; achenes 3–4.5 mm long. Two varieties occur in Utah.

1. Flowering stems usually definitely swollen below the first branches of the inflorescence and often upward as well, glabrous or sometimes tomentose; plants of Kane and Washington counties .... *E. racemosum* var. *zionis*
— Flowering stems not at all or only occasionally somewhat swollen, tomentose or occasionally glabrous; plants widespread .... *E. racemosum* var. *racemosum*

Var. ***racemosum*** Sagebrush, pinyon-juniper, mountain brush, ponderosa pine, aspen, and spruce-fir communities at 1525 to 2745 m in Beaver, Cache, Davis, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, Piute, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Utah, Washington, and Wayne counties; Nevada, Colorado, Arizona, and New Mexico; 108 (xiv).

Var. ***zionis*** **(J. T. Howell) Welsh** comb. nov. [based on: *E. zionis* J. T. Howell Leafl. W. Bot. 2: 253. 1940]. Zion Buckwheat. Mountain brush, juniper-manzanita, and ponderosa pine communities at 1340 to 1830 m in Kane and Washington (type from Zion National Park) counties; Arizona; 9 (v). Specimens are known that grade morphologically with var. *racemosum*; i.e., plants with glabrous stems are essentially nonfistulose and some with fistulose stems are tomentose throughout. The phase with scarlet flowers from nearby in Arizona are very similar to specimens of var. *racemosum* with deep rose-colored flowers. The variety might ultimately be discovered in Utah, and is regarded herein as ***E. racemosum*** **var. *coccineum* (J. T. Howell) Welsh** comb. nov. [based on: *E. zionis* var. *coccineum* J. T. Howell Leafl. W. Bot. 2: 253. 1940].

Eriogonum salsuginosum **(Nutt.) Hook.** Smooth Buckwheat. [*Stenogonum salsuginosum* Nutt.]. Annuals, mainly 3–26 cm tall, clump-forming, 3–40 cm wide; leaves basal and cauline (foliose bracteate); blades 2–20 mm long, 2–12 mm wide, spatulate to oblanceolate, obovate, or linear, tapering to broad petioles 2–20 mm long or sessile, glabrous on both sides; inflorescence more or less dichotomous, glabrous or minutely glandular; involucres sessile or on stipes to 4 cm long, these curved-ascending, broadly campanulate, in 2 whorls, each 3-lobed; flowers yellow, 1.5–3 mm long, puberulent, the segments lanceolate; achenes 2–2.5 mm long. Shadscale, mat-atriplex, and pinyon-juniper communities at 1370 to 2760 m in Carbon, Daggett, Duchesne, Emery, Garfield, San Juan, and Uintah counties; Wyoming, Colorado, Nevada, Arizona, and New Mexico; 48 (viii).

Eriogonum scabrellum **Reveal** Westwater Buckwheat. Annuals, mainly 20–60 cm tall; leaves all basal, usually persistent at anthesis and beyond; blades 1–6 cm long and about as wide, orbicular to suborbicular, cordate basally, the margin strongly undulate-crisped, tomentose on one or both sides; petioles 8–50 mm long; inflorescences spreading-ascending to umbrellalike, tomentose and glandular; involucres sessile, erect or decurved, on usually decurved branchlets, obconic, 1.5–2.5 mm long, with 5 acute teeth; flowers white or suffused with pink or red, 1.5–2.2 mm long, the outer segments obovate, the inner ones narrower; achenes 1.8–1.8 mm long. Salt desert shrub communities at ca 1220 to 1740 m in Garfield, Grand (type from Westwater), Kane, and San Juan counties; Colorado and New Mexico; 7 (i).

Eriogonum shockleyi **Wats.** Shockley Buckwheat. [*E. pulvinatum* Small, type from Milford; *E. longilobum* Jones, type from near Price]. Pulvinate-caespitose, scapose, mound-forming perennials, mainly 2–5 cm tall, 5–40 cm across or more, from a woody, pluricipital caudex, the branches clothed with marcescent leaf bases and terminated by rosettes; leaf blades 2–12 mm long, 1–6 mm wide, obovate, oblanceolate, elliptic, or spatulate, tomentose on one or both sides; petioles 1–10 mm long, or lacking; inflorescences capitate; involucres sessile, campanulate, 2–6 mm long, tomentose, with 5 (or more) ovate to lanceolate lobes; flowers white, cream, yellow, or suffused with red, 2.5–4.5 mm long, pilose, the segments oblong to obovate; achenes 2.5–3.5 mm long. Blackbrush, shadscale, mixed desert shrub, sagebrush, and pinyon-juniper communities, often on fine-textured substrates, at 1280 to 1955 m in Beaver, Box Elder, Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, San Juan, Sevier, Tooele, Uintah, and Wayne counties; Idaho to Colorado, south to California, Arizona, and New Mexico; 107 (xv). Specimens from Utah have been treated in two varieties; i.e., var. *longilobum* (Jones) Reveal, with larger, more deeply cut involucres, occupying eastern Utah, and var. *shockleyi* with shorter, less deeply cut involucres, occupying western Utah. Some of the plants from eastern Utah do have large involucres, but many do not. A large number of plants from western Utah have yellow flowers, but very few from eastern Utah bear yellow flowers, indicating a difference in gene frequency. A conservative interpretation is indicated.

Eriogonum soredium **Reveal** Frisco Buckwheat. Densely matted, pulvinate-caespitose, scapose, mound-forming perennials, mainly 2–4 cm tall, 10–50 cm across, from a pluricipital caudex, the branches clothed with marcescent leaf bases and terminated by rosettes; leaves 2–5 mm long, 0.7–2 mm wide, elliptic to oblong, white-tomentose on both surfaces, revolute; petioles 0.6–3 mm long; inflorescences capitate, tomentose; involucres sessile, obconic, 1.5–2.5 mm long, obscured by a dense tomentum, with 4 or 5 teeth; flowers white or suffused with pink, 2–3 mm long, glabrous, the outer segments obovate, the inner ones narrower; achenes 2–2.5 mm long. Sagebrush and juniper communities, on white limestone outcrops, at ca 2010 to 2230 m in Beaver County; endemic; 5 (ii).

Eriogonum spathulatum **Gray** Sevier Buckwheat. [*E. nudicaule* ssp. *ochroflorum* Stokes]. Perennial herbs, 10–40 cm tall, from a branching caudex; leaves subbasal, at least some internodes apparent, but obscured by a dense tomentum; blades 1–8 cm long, 3–15 mm wide, obovate to spatulate, elliptic, or linear, usually 1.5–5 times longer than wide or more, tomentose on one or both sides, acute to cuneate basally; petioles 3–30 mm long; inflorescences tomentose or glabrous, more or less trichotomous, the branches ascending; involucres sessile, clustered at branch ends, obconic, 2–4 mm long, tomentose or glabrous, with 5 acute teeth; flowers white or yellow, 2–3.5 mm long, glabrous, the segments oblong; achenes 2–3.5 mm long. Two more or less geographically correlated varieties are present.

1. Flowers yellow; leaf blades mainly less than twice as long as broad .... *E. spathulatum* var. *natum*

— Flowers white, or rarely yellow; leaf blades usually more than twice longer than broad .... *E. spathulatum* var. *spathulatum*

Var. *natum* (Reveal) Welsh comb. nov. [based on: *E. natum* Reveal in Welsh, Atwood, and Reveal Great Basin Nat. 35: 363. 1975]. Son Buckwheat. Shadscale community on ancient marly playa remnants at 1440 to 1500 m in Millard (type from 43 mi SW of Delta) County; endemic; 10 (ii).

Var. *spathulatum* [*E. nudicaule* ssp. *ochroflorum* Stokes, type from Clear Creek Canyon, Sevier County]. Greasewood, shadscale, rabbitbrush, ephedra, and pinyon-juniper communities at 1405 to 2135 m in Beaver, Millard, Sanpete, Sevier (type from Sevier River Valley), and Wayne counties; endemic; 47 (xiv). Both this and var. *natum* show affinities with *E. brevicaule* var. *laxifolium* (q.v.), especially through the densely hairy, low elevation *cottamii* phase, whose distribution is immediately adjacent to the north. The relationship is also through the *laxifolium* phase proper northeastward in Sanpete County. Plants with glabrous inflorescences and involucres from the vicinity of Frisco and the Shauntie Hills in Beaver County have about the same integrity as does var. *ammophilum* of the *E. nummulare* complex. Probably they have one parent in common, i.e., *E. batemanii* var. *eremicum*, but the other putative parent is different. These glabrous plants are similar to phases of *E. panguicense*, but the inflorescences are consistently branched.

Eriogonum subreniforme **Wats.** Stokes Buckwheat. [*E. filicaule* Stokes, type from Springdale]. Annuals, mainly 5–40 cm tall; leaves all basal; blades 4–30 mm long and about as broad or broader, orbicular to reniform, tomentose on one or both sides, truncate to cordate basally; petioles 6–60 mm long; inflorescence more or less trichotomous, glabrous, the branches ascending to spreading; involucres on filiform stipes mostly 3–25 mm long, glabrous, obconic, mostly 0.5–1 mm long, with 5 acute teeth; flowers white to rose, 1–2 mm long, glabrous or distinctly puberulent, the segments elliptic to lance-elliptic or spatulate; achenes 1.5–2 mm long. Creosote bush, shadscale, eriogonum, sagebrush, and pinyon-juniper communities at 850 to 1985 m in Garfield, Kane, and Washington (type from St. George) counties; Arizona and New Mexico; 17 (ii). Specimens from Garfield and Kane counties have glabrous flowers.

Eriogonum thomasii **Torr.** Thomas Buckwheat. [*E. minutiflorum* Wats.]. Annuals, mainly 5–30 cm tall; leaves all basal; blades 4–20 mm long and about as wide, orbicular to subreniform, tomentose on one or both sides, obtuse to subcordate basally; petioles 3–30 mm long; inflorescences more or less polychotomous, glabrous, the branches spreading to ascending; involucres on stipes mainly 3–30 mm long, glabrous, obconic to campanulate, 0.6–1.2 mm long, the 5 teeth obtuse; flowers yellow, 0.8–2 mm long, hispidulous near the base, the outer segments becoming saccate at maturity, the inner ones narrow and not saccate; achenes ca 1 mm long. Creosote bush community at ca 850 to 915 m in Washington County; California, Nevada, Arizona, and Mexico; 6 (i).

Eriogonum thompsonae Wats. Ellen Buckwheat. [*E. corymbosum* var. *matthewsiae* Reveal, type from Springdale]. Perennial subshrubs or shrubs, mainly 2–8 dm tall, clump forming; leaves subbasal or definitely cauline; blades 10–60 mm long, 8–28 mm wide, oblong to elliptic, lanceolate or ovate, tomentose on one or both sides, the margins entire, flat or undulate and sometimes crisped; petioles 1.5–10 cm long; inflorescences more or less trichotomous, glabrous or less commonly tomentose, the branches spreading to ascending; involucres sessile, narrowly obconic, 2.5–3.8 mm long, glabrous or tomentose, the teeth rounded and more or less hyaline; flowers yellow or white, 2.5–4 mm long, glabrous, the segments oblong or obovate; achenes 2–3 mm long. Blackbrush, salt desert shrub, and pinyon-juniper communities, mainly on Chinle and Moenkopi formations, at 1125 to 1830 m in Kane and Washington counties; Arizona, a Mohave Strip endemic; 32 (iii). The *thompsonae* complex consists of a series of morphological subunits, each more or less distinctive, but only arbitrarily separable. They are based on application of the 2^n formula, where "n" equals the number of characters contrasted, i.e., yellow or white flowers with subscapose or caulescent habit. Plants with yellow flowers and subscapose habit are var. *thompsonae* (type from near Kanab); those with white flowers and subscapose habit are var. *albiflorum* Reveal (type from W of Virgin; *E. corymbosum* var. *matthewsiae*, in part); those with yellow flowers and caulescent habit are *E. corymbosum* var. *aureum*, in part (Shivwits phase); and those with white flowers and caulescent habit are *E. corymbosum* var. *matthewsiae* (Springdale phase), at least in part. The yellow flowers of the Shivwits phase seem to have been secondarily derived from *E. corymbosum* var. *aureum* (*E. aureum* Jones, in a strict sense), where occasional specimens have loosely tomentose inflorescences and the involucres are shortly obconic as in var. *glutinosum*. In other specimens of the Shivwits phase the narrowly obconic involucres are essentially like those of var. *albiflorum*. The recognition of any of these phases at taxonomic rank is problematical because of intermediates connecting most if not all of them. A key is provided for the main kinds observed. The use of names applied in other taxa does not indicate nomenclatural combination, and none is intended or implied herewith.

1. Flowers yellow 2
— Flowers white 3
2(1). Plants subscapose, with long petioles and oblong-oval leaf blades; growing east of Kanab and in Washington County .... *E. thompsonae* var. *thompsonae*
— Plants definitely caulescent, with petioles short and leaf blades oval to oblong or lanceolate .... "Shivwits phase"
3(1). Plants subscapose, with long petioles and elliptic to oblong-oval leaf blades; known from eastern Washington County and transitional to the next .... *E. thompsonae* var. *albiflorum*
— Plants caulescent, with long or short petioles and leaf blades oval to oblong or lanceolate .... "Springdale phase"

Eriogonum trichopes **Torr.** Slender-stipe Buckwheat. [*E. trichopodum* Torr. in DC.; *E. trichopodum* var. *minus* Benth. in DC.]. Annuals, 8–45 cm tall; leaves all basal; blades mainly 5–30 mm long, 4–25 mm wide, oval to orbicular, hirtellous on one or both sides, obtuse to cordate basally, entire to undulate-crisped; petioles 3–40 mm long or more; peduncles and primary rays of inflorescence inflated or not; inflorescence polychotomous; involucres borne on capillary stipes 3–18 mm long, obconic to campanulate, 0.4–1 mm long, glabrous, 4-lobed; flowers yellowish, 1–2 mm long, strigulose, the segments lance-ovate; achenes 1.5–2 mm long. Warm desert shrub communities at 760 to 980 m in Washington County; Nevada and Callifornia to New Mexico, south to Mexico; 10 (i). This species simulates the annual phase of *E. inflatum* in having inflated stems in some plants. The usually more numerous branches from the lowest node of the inflorescence, and flowers and involucres that average smaller, are diagnostic.

Eriogonum tumulosum **(Barneby) Reveal** Woodside Buckwheat. [*E. villiflorum* var. *tumulosum* Barneby, type from SW of Woodside]. Pulvinate-caespitose, mound-forming, herbaceous perennials from a pluricipital caudex and woody taproot, the caudex branches clothed with persistent leaves and bases, the roots with shaggy castaneous to blackish bark; leaves 3–7 mm long, 0.7–1.5 mm wide, oblanceolate to elliptic, tomentose to pilose on both surfaces, revolute; petioles very short; scapes to ca 1 cm long or lacking; inflorescences capitate; involucres campanulate, 2–4 mm long, villous, 7- to 10-lobed; flowers white or suffused with pink, 3–4 mm long, pilose, the segments oblong to oblanceolate; achenes ca 2 mm long. Mixed desert shrub and pinyon-juniper communities at 1525 to 2170 m in Duchesne, Emery, and Uintah counties; Colorado; a Colorado Plateau endemic; 16 (ii).

Eriogonum umbellatum **Torr.** Sulfur Buckwheat. Perennial herbs or subshrubs, mat forming, mainly 1–10 dm across; vegetative stems persistent, the branches woody and usually more or less clothed with persistent ashy, castaneous, or blackish leaves and bases; flowering stems scapose, arising from rosette-like stem apices, mainly 10–60 cm tall; leaf blades 4–30 mm long, 2–20 mm wide, ovate to oval, elliptic, lanceolate, or oblanceolate, tomentose or glabbrous on one or both sides, flat or nearly so; petioles 2–15 mm long; inflorescence umbellate (or compound) or capitate, often immediately subtended by foliose bracts; involucres terminating rays or sessile, obconic to campanulate, the tube 2–6 mm long and 1.5–10 mm wide, the lobes 1–6 mm long; flowers creamy white to yellow and often suffused with red or purple, 2.5–10 mm long (including the stipitate base), the segments spatulate to ovate; achenes 2–5 mm long. This species is a portion of a huge assemblage occupying much of the western U.S. There are four more or less geographically correlated varieties present.

1. Flowers creamy white .... *E. umbellatum* var. *majus*
— Flowers yellow 2
2(1). Inflorescences of compound umbels, at least some; plants mainly of middle to lower elevations in the southern two-thirds of Utah .... *E. umbellatum* var. *subaridum*
— Inflorescences merely umbellate or capitate 3
3(2). Inflorescences capitate or rarely some branched; leaves glabrous on both sides; plants of high elevations .... *E. umbellatum* var. *porteri*
— Inflorescences umbellate; leaves variously pubescent, sometimes as above; plants of moderate to high elevations .... *E. umbellatum* var. *umbellatum*

Var. *majus* Hook. Cream Buckwheat. [*E. subalpinum* Greene; *E. umbellatum* var. *subalpinum* (Greene) Jones; *E. umbellatum* ssp. *subalpinum* (Greene) Stokes; *E. heracleoides* var. *subalpinum* (Greene) R. J. Davis; *E. umbellatum* ssp. *majus* (Hook.) Piper; *E. aridum* Greene; *E. umbellatum* ssp. *aridum* (Greene) Stokes; *E. umbellatum* var. *aridum* (Greene) C. L. Hitchc.; *E. umbellatum* var. *dicrocephalum* Gandg.; *E. umbellatum* var. *desereticum* Reveal, type from Mt. Timpanogos]. Sagebrush, mountain brush, pinyon-juniper, Douglas fir-white fir, aspen, lodgepole pine, and spruce-fir communities at 1495 to 3420 m in Beaver, Box Elder, Cache, Carbon, Daggett, Davis, Duchesne, Garfield, Juab, Millard, Rich, Salt Lake, Sanpete, Sevier, Summit, Tooele, Wayne, and Weber counties; Canada, south to California and Nevada; 73 (vi). This plant forms apparent hybrids (Neese 14620 A-E BRY) with *E. heracleoides*. It is also identical, except for flower color, with var. *umbellatum* and has a similar sequence of pubescence forms.

Var. *porteri* (Small) Stokes Porter Buckwheat. [*E. porteri* Small, type from Bear River Canyon, Summit County]. Ponderosa pine, aspen, spruce-fir, lodgepole pine, and alpine meadow and talus communities at 2500 to 3700 m in Beaver, Duchesne, Iron, Sanpete, Sevier, Summit, and Uintah counties; Nevada and Colorado; 41 (xi).

Var. ***subaridum*** Stokes Arid Buckwheat. [*E. umbellatum* ssp. *subaridum* (Stokes) Munz; *E. biumbellatum* Rydb., type from Fish Lake; *E. ferrissii* A. Nels.; *E. umbellatum* ssp. *ferrissii* (A. Nels.) Stokes]. Sagebrush, mountain brush, pinyon-juniper, and Douglas fir communities at 1370 to 2745 m in Beaver, Emery, Garfield, Iron, Juab, Kane, Millard, San Juan, Sanpete, Sevier, Summit, Tooele, Washington, and Wayne counties; Colorado, Arizona, Nevada, and California; 79 (xvi). Occasional specimens share features, especially simple inflorescences and pubescence phases, with other varieties of the species.

Var. ***umbellatum*** [*E. luteum* Small ex Rydb.; *E. rydbergii* Greene; *E. cupreum* Gand.; *E. glaberrimum* var. *aureum* Gand.; *E. umbellatum* var. *aureum* (Gand.) Reveal; *E. neglectum* Greene; *E. azaleastrum* Greene; *E. umbelliferum* Small; *E. umbellatum* var. *umbelliferum* (Small) Stokes; *E. marginale* Gand.; *E. umbellatum* var. *intectum* A. Nels; *E. umbellatum* var. *glabratum* Stokes, type from Huntington Canyon]. Sagebrush, mountain brush, pinyon-juniper, ponderosa pine, white fir, aspen, spruce-fir, and alpine meadow communities at 1765 to 3450 m in Beaver, Box Elder, Carbon, Daggett, Duchesne, Emery, Grand, Juab, Millard, Piute, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Wayne counties; Washington to Montana, south to California, Nevada, and Colorado; 111 (xv).

Eriogonum villiflorum Gray Gray Buckwheat. Pulvinate-caespitose, mound-forming, herbaceous perennials from a pluricipital caudex and woody taproot, the caudex branches clothed with persistent ashy to castaneous or blackish leaf bases and with shaggy blackish bark; leaves 4–15 mm long, 0.7–2 mm wide, oblanceolate to elliptic, villous-pilose on both sides, more or less revolute; petioles very short; scapes mainly 1–5 cm long; inflorescences subcapitate to shortly umbellate; involucres sessile or short-stipitate, campanulate, 3–5 mm long, villous-pilose, with 6–10 lobes; flowers white or suffused with pink, 3–4 mm long, pilose, the segments oblong; achenes 2–3 mm long. Sagebrush, pygmy sagebrush, mixed desert shrub, and pinyon-juniper communities at 1555 to 2350 m in Beaver, Juab, Millard, and Sanpete counties; Nevada; a Great Basin endemic; 17 (iii).

Eriogonum wetherillii **Eastw.** Wetherill Buckwheat. [*E. sessile* Stokes ex Jones; *E. filiforme* L. O. Williams, type from near Hanksville]. Annuals, 5–30 cm high, ultimately forming cushionlike, intricately branched clumps, mainly 8–40 cm wide; leaves all basal; blades 4–40 mm long and about as wide, orbicular to oval, tomentose on one or both sides, obtuse to subcordate basally; petioles 5–50 mm long; inflorescences intricately branched, glabrous, ultimately gray- to red-purple; involucres on filiform stipes, mainly 3–16 mm long or sessile, obconic, glabrous, 0.5–1 mm long, with 4 teeth; involucres yellow, soon suffused with red, 0.6–1.5 mm long, glabrous, the segments elliptic to obovate; achenes 0.6–1 mm long. Blackbrush, shadscale, mixed desert shrub, and pinyon-juniper communities (and often along roadsides) at 1125 to 2135 m in Emery, Garfield, Grand, Kane, San Juan (type from along the San Juan River) , Sevier, and Wayne counties; Colorado, New Mexico, and Arizona; 68 (xii).

Eriogonum wrightii **Torr. in DC.** Wright Buckwheat. Shrubs, mainly 2–5 dm tall; leaves caulescent, mainly 5–25 mm long and 3–10 mm wide, elliptic to oblanceolate, tomentose on both sides, plane or more or less revolute; petioles 1–6 mm long; inflorescence erect-ascending, tomentose, more or less racemose; involucres sessile, obconic, tomentose, 2–4 mm long, with 5 teeth; flowers white or suffused with pink, 3–4 mm long, glabrous, the segments obovate; achenes 2–3 mm long. Pinyon-juniper and mountain brush communities at ca 1190 m in Washington County (upper Beaverdam Wash); California to Texas, south to Mexico; 3 (i).

OXYRIA Hill

Perennial, subrhizomatous herbs, from long taproots; leaves simple, alternate or mostly basal; stipules sheathing; flowers numerous, borne in panicles, not subtended by an involucre; perianth of 4 sepaloid segments, glabrous; stamens 6; pistil 2-carpelled, the ovary 1-loculed, 1-ovuled; styles 2, short, the stigmas fringed; fruit a flattened, wing-margined achene.

Oxyria digyna **(L.) Hill** Mountain sorrel. [*Rumex digynus* L.]. Plants mainly 5–35 cm tall, the herbage often reddish tinged; stems usually simple, the juice acrid; leaves mostly basal; petioles 1–15 cm long; blades 5–50 mm long and as wide or wider, reniform to orbicular, cordate basally; panicles 2–20 cm long; perianth 1–2.5 mm long, the 2 segments at achene edges more slender than those on the flat sides; achenes flattened, 3–6 mm broad, prominently winged. Lodgepole pine, spruce-fir, and alpine meadow communities, often in Talus, at 2560 to 3965 m in Beaver, Box Elder, Cache, Daggett, Duchesne, Piute, Salt Lake, San Juan, Sanpete, Summit, Uintah, Utah, and Weber counties; Alaska and Yukon, east to Labrador, south to California, Arizona, and New Mexico; circumboreal; 38 (ix).

OXYTHECA Nutt.

Annuals; stems dichotomously branched; leaves basal; bracts connate, in 3's, foliaceous; involucres few-flowered, stipitate, more or less campanulate, 4-lobed, the lobes awn tipped; flowers pedicellate; perianth 6-parted; stamens 9; achenes ovoid.

Oxytheca perfoliata **T. & G.** [*Eriogonum perfoliatum* (T. & G.) Stokes]. Plants 6–20 cm tall or more, erect or spreading-ascending; leaves basal and cauline (leafy bracteate), the basal ones 1–4 cm long, spatulate to oblanceolate, sparingly hirsute to glabrous, ciliate; inflorescences short-pedunculate, then dichotomous or trichotomous, with each node bearing a connate-perfoliate, foliaceous, 3-lobed bract ca 1–2 cm wide, the lobes spinose tipped; internodes of inflorescence more or less stipitate-glandular; involucres solitary, obconic, 3–6 mm long, including spines, 4-lobed, each lobe spinose tipped; flowers several; cream to whitish, ca 1.5 mm long, coarsely strigose, the segments lanceolate; achenes ca 2 mm long. Warm desert shrub communities at ca 950 m in Washington County; Arizona, Nevada, and California; 1 (0).

POLYGONUM L.

Plants annual, biennial, or perennial herbs from taproots or rhizomes; leaves alternate, cauline or basal; stipules sheathing; flowers solitary or clustered in leaf axils or in axillary or terminal spikelike racemes or panicles, not subtended by a regular involucre; perianth of 5 petaloid (or sepaloid) segments; stamens 8 (5 and 3) or lacking; pistils usually 3-carpelled, the ovary 1-loculed, 1-ovuled; styles 2 or 3, often very short; achenes lens shaped or 3-angled.

1. Leaves with subcordate, cordate, or hastate bases; flowers in axillary racemes or panicles; plants cultivated ornamentals, escaping and persisting, or weed 2

— Leaves various but not cordate or hastate basally; flowers variously arranged but not as above; plants indigenous or adventive, weedy or not 4

2(1). Stems not twining; leaves broadly obovate, obtuse to subcordate basally; plants clump-forming, cultivated ornamentals, escaping and persisting .... *P. cuspidatum*

— Stems twining; leaves cordate to hastate; plants sprawling or twining on other plants or structures 3

3(2). Plants perennial; flowers showy, whitish; fruit broadly winged; cultivated ornamentals, escaping and persisting .... *P. aubertii*

— Plants annual; flowers not showy, greenish; fruit not winged; adventive weedy species .... *P. convolvulus*

4(1). Stems erect, from an expanded to somewhat bulbous caudex; leaves mostly basal; flowers in terminal spicate racemes; plants mostly of higher elevations 5

— Stems of various habit, but not from a caudex, or, if so, the plants otherwise different from above; flowers axillary or in axillary and terminal spikelike racemes or panicles 6

5(4). Racemes slender, mainly 4–6 mm thick, the lower flowers at least replaced by bulblets .... *P. viviparum*

— Racemes mainly 10–25 mm thick, the flowers not replaced by bulblets .... *P. bistortoides*

6(5). Leaves not jointed at the base; flowers in terminal and (or) axillary spikes or racemes 7

— Leaves with a hingelike joint at the point of attachment of leaf base with sheath; flowers in small, axillary clusters or solitary 11

7(6). Inflorescences all terminal, usually solitary; plants perennial, aquatic or semiaquatic to terrestrial; flowers bright pink .... *P. amphibium*

— Inflorescences not all terminal, at least some axillary; plants mostly annual, seldom aquatic (but sometimes so); flowers pink, green, or white 8

8(7). Stipular sheaths lacking marginal bristles (or merely short-ciliate); veins of the outer pair of perianth segments branched and recurved at the tip .... *P. lapathifolium*

— Stipular sheaths usually with well-developed marginal bristles; veins of the outer pair of perianth segments not branched and recurved at the tip 9

9(8). Plants perennial from rhizomes, growing in or near water; spikes slender, mostly less than 5 mm broad, often paired; not definitely known from Utah, but to be expected .... *P. hydropiperoides* Michx.

— Plants annual from taproots, growing in moist sites, but not aquatic; spikes slender to thick, not or seldom paired 10

10(9). Mature perianth glandular-punctate, greenish to white (or pinkish); spikes slender, arching, interrupted near the base .... *P. hydropiper*

— Mature perianth not glandular-punctate, pink to purplish; spikes dense, erect or nearly so, not or rarely interrupted .... *P. persicaria*

11(6). Flowers in terminal, leafy-bracteate spikes; plants mainly less than 10 cm tall .... *P. kelloggii*

-- Flowers in axillary clusters or solitary, or in terminal spikes with bracts much reduced; plant height various 12

12(11). Leaves ovate to broadly elliptic, scarcely reduced upward; plants mainly less than 10 cm tall .... *P. minimum*

— Leaves linear to narrowly elliptic, lanceolate, or oblanceolate, more or less reduced upward; plant height various 13

13(12). Flowers borne in elongate, spikelike racemes; leaves much reduced and bractlike upward; plants usually erect and with branches erect-ascending .... *P. ramosissimum*

— Flowers borne in axils of foliage leaves, these sometimes reduced but not especially bracteate upward; plants of various habit 14

14(13). Plants mainly prostrate; leaves mostly flat and with prominent lateral veins, often deciduous in fruit .... *P. aviculare*

— Plants mainly erect or ascending; leaves flat to revolute, the veins inconspicuous, usually persistent .... *P. douglasii*

Polygonum amphibium **L.** Water Smartweed. [*P. coccineum* Muhl. in Willd.]. Perennial aquatic or terrestrial, rhizomatous or stoloniferous herbs, the herbage coarsely strigose to glabrous or stipitate-glandular; stems prostrate (often floating) or erect; leaf blades mainly 3–18 cm long, 1–6 cm wide, lanceolate to oblong or elliptic, acute to alternate or rounded apically, obtuse to truncate basally; petioles 0.5–7 cm long; stipules cylindric, 0.5–3 cm long, glabrous to coarsely strigose; panicles 1 or 2, spikelike, 1–8 cm long, the peduncles glabrous, glandular, or strigose and also more or less glandular; pedicels 1–2 mm long; flowers bright pink, 4–5 mm long, the segments oblong, subequal; stamens 8, exserted; style 2–4 mm long; achenes lenticular 2–3 mm long, brown, shining or dull. Springs, streams, ponds, lakes, reservoirs, and irrigation canals at 1340 to 2865 m in Cache, Daggett, Duchesne, Garfield, Millard, Piute, Salt Lake, Sevier, Uintah, Utah, and Weber counties; widely distributed in North America; cosmopolitan (except Australia?); 47 (v). Traditional separation of this taxon into two species on the basis of pubescence and panicle differences is not supported by the cline of variation connecting the distinctive extremes.

Polygonum aubertii **L. Henry.** Silver Lace-vine. Perennial, twining herbs; stems mainly 2–7 m long or more; herbage glabrous or scabrous; ocrea soon deciduous, the margin not ciliate; leaf blades 1–8 cm long and 1–6 cm wide, cordate-ovate, cordate basally, attenuate to acuminate apically; petioles 0.5–5 cm long; panicles open, axillary or terminal, 5–15 cm long or more; flowers usually white, 7–10 mm long, including the attenuate winged base, fragrant; fruit lenticular (?), seldom formed. Cultivated ornamental, escaping and persisting in Utah County; introduced from China; 2 (0)

Polygonum aviculare **L.** Knotweed; Chivalry-grass; Dishwater-grass. Annuals, prostrate to ascending or erect, the stems striate, terete or angled, mostly 1–10 dm long; leaves usually not crowded, 5–40 mm long and 2–10 mm wide, oblong to elliptic or oblanceolate, smaller on the branchlets than on the main stem, acute to obtuse or rounded, the blade sessile or short-petiolate above the basal joint; stipules shredded, 3–6 mm long; flowers 1–5 axillary; pedicels included or shortly exserted; perianth 2–3 mm long, united ca one-third the length, 5-lobed, the lobes greenish with white or pink edges, the outer lobes only slightly broader than the inner; styles 3; achenes 3-angled, brown. Weedy species of open sites at 760 to 3085 m in probably all Utah counties; widespread in most continents; 59 (vii). The plants tolerate trampling and similar abuse that forces other plants to yield way to this vigorous species.

Polygonum bistortoides **Pursh** American Bistort. [*P. bistorta* var. *oblongifolium* Meissn. in DC.; *P. bistorta* var. *linearifolium* Wats. Perennials, erect, from thickened bulblike bases and rhizomes, the stems mainly 1–8 dm tall; basal leaves well developed, mainly 5–30 cm long, the blades 2–20 cm long and 0.3–3.5 cm wide, lanceolate to elliptic or linear, attenuate to obtuse or rounded apically, cuneate to obtuse basally; petioles usually well developed, not jointed; stipules mainly 1.5–8 cm long, sometimes flaring apically; cauline leaf blades reduced upward; flowers numerous, borne in terminal spikelike racemes, 1–7 cm long; perianth 4–6 mm long; connate only near the base, white or sometimes pinkish, the segments about equal in size; stamens 8, exserted; styles 3, exserted; achenes brown, shining, ca 4 mm long. Aspen, lodgepole pine, and spruce-fir communities, usually in moist meadows, at 2070 to 3510 m in Beaver, Cache, Daggett, Duchesne, Emery, Garfield, Iron, Juab, Kane, Millard, San Juan, Sanpete, Sevier, Summit, Uintah, Wasatch, Wayne, and Weber counties; British Columbia to Montana, south to California, Arizona, and New Mexico; 68 (x). This species differs in degree only from *P. bistorta* of the Old World and Alaska-Yukon-Mackenzie. The synonyms indicate the views of some previous workers in this genus. Additional work might indicate a more conservative view than that followed here.

Polygonum convolvulus **L.** Black Bindweed. Annuals, erect (when young) or soon prostrate or twining, the stems 1–15 dm long or more; leaves with long petioles not jointed basally, the blades 1–8 cm long (from sinus to apex), 0.7–5 cm wide, sagittate-ovate, acuminate; stipules 2–5 mm long, shredded and soon deciduous; flowers few to many, borne in axillary or terminal racemes; perianth 3–4.5 mm long, greenish, 5-lobed, the outer lobes keeled; styles 3-cleft; achenes 3-angled, black, usually shining. Weedy species of gardens, fields, and other open habitats at 850 to 1680 m in Cache, Salt Lake, Sevier, Utah, and Washington counties; widespread in North America; adventive from Europe; 11 (0).

Polygonum cuspidatum Sieb. & Zucc. Fleece-flower. [*P. zuccarinii* Small]. Perennial, dioecious, erect or ascending herbs, mainly 8–15 dm tall; leaves petiolate, the blades mostly 5–15 cm long and 3–10 (12) cm wide, ovate, cuneate to truncate or subcordate basally, abruptly acuminate apically; stipules 4–8 mm long, soon deciduous; flowers 4–5 mm long or more, including the winged, stipelike base, cream to greenish, functionally imperfect, enlarging in fruit; styles 3; achenes 3-angled, black, smooth, shining, ca 3 mm long. Cultivated ornamentals, escaping and persisting, at 1220 to 1830 m in Duchesne, Salt Lake, and Utah counties; widely grown in the U.S.; introduced from Asia; 5 (0).

***Polygonum douglasii* Greene.** Douglas Knotweed. Annuals, mainly 3–45 cm tall or more, erect or ascending; leaves 6–50 mm long, 1–8 mm wide, linear to oblong, lanceolate or oblanceolate, gradually reduced upward, jointed at the base; stipules lacerate, 3–12 mm long; flowers axillary, usually 1–4 per node, the pedicels erect or reflexed, 14 mm long; perianth 2–4.3 mm long, the segments green with white or pink to reddish margins, or white to pink overall, united only near the base;a chenes 3-angled, black, smooth and shining, 2.5–3.5 mm long. Two rather well-defined but largely sympatric varieties are present in Utah.

1. Flowers deflexed, stipitate above a joint at pedicel apex, the stipe 0.1–0.2 mm long and persistent on the flower base .... *P. douglasii* var. *douglasii*

— Flowers erect, not stipitate, the base sessile on the joint, dehiscing without a peglike stipe at the base .... *P. douglasii* var. *johnstonii*

Var. ***douglasii*** Sagebrush, mountain brush, pinyon-juniper, ponderosa pine, Douglas fir-white fir, aspen, lodgepole pine, and spruce-fir communities at 1705 to 3145 m in Cache, Carbon, Daggett, Duchesne, Garfield, Grand, Juab, Kane, Millard, Salt Lake, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Weber counties; widely distributed in North America; 56 (v).

Var. ***johnstonii* Munz** Sawatch Knotweed. [*P. sawatchense* Small; *P. utahense* Brenkle & Cottam, type from 6 mi N of Escalante]. Pinyon-juniper, mountain brush, sagebrush, and spruce-fir communities at 1675 to 2625 m in Beaver, Carbon, Daggett, Duchesne, Garfield, Grand, Iron, Juab, Kane, Millard, Piute, Rich, San Juan, Sevier, Summit, Tooele, Uintah, Utah, and Washington counties; Washington to North Dakota, south to California, Arizona, and Colorado; 44 (viii). A phase with flowers almost completely white or pink, which tend to open wide (apparently *P. utahense*, sens. str.), occurs in sandy soils in the ponderosa pine and adjacent plant communities in eastern Washington and western Kane and Garfield counties. Possibly these plants are worthy of taxonomic recognition. More work is indicated, but similar plants occur elsewhere within the range of var. *johnstonii*.

***Polygonum hydropiper* L.** Water-pepper. Plants annual (sometimes perennial?), the stems occasionally rooting at the nodes, mainly 3–8 dm tall; leaves with short petioles or else subsessile, not jointed at the base, the blades 3–10 cm long, 0.5–3 cm broad, lanceolate to elliptic, acute to acuminate apically, acute to cuneate basally, sparsely strigose to glabrous, ciliate; stipules 8–15 mm long, not shredded, strigose to glabrous, ciliate with long bristles; flowers several to many, borne in terminal and usually also in lateral, spikelike, interrupted racemes 2–8 cm long; perianth 2.5–4 mm long, glandular-dotted, united ca one-third the length, usually 4-lobed, the lobes greenish with white or pink margins; styles 2 or 3, distinct; achenes lens shaped or 3-angled, brown. Irrigation ditches, roadsides, and bottomlands at ca 1340 to 1375 m in Salt Lake and Utah counties; widespread in North America; adventive from Europe; 3 (0). The herbage has a peppery flavor.

***Polygonum kelloggii* Greene** Kellogg Knotweed. Annuals, erect or ascending, 1–9 cm tall, the stems angled, simple or branched; leaves 3–20 (25) mm long, 0.5–2 mm wide, usually crowded and bracteate upward (surpassing the flowers), and sometimes white margined, sessile or nearly so, jointed at the base; stipules lacerate, 2–7 mm long; pedicels mostly included; perianth 1.5–2.5 mm long, connate in lower one-third, the 5 lobes subequal or the outer ones largest, green with white or pink margins; stamens 8, the 5 outer ones with linear filaments and usually abortive anthers; stigmas 3; achenes 3-angled, 1.5–2 mm long, yellow to brownish, shining and smooth or brown and dull. Mountain brush, sagebrush, ponderosa pine, meadows, lodgepole pine, aspen, and spruce-fir communities at 1830 to 3235 m in Cache, Daggett, Duchesne, Emery, Garfield, Salt Lake, San Juan, Sevier, Summit, Uintah, and Wasatch counties; British Columbia to Montana, south to California, Arizona, and Colorado; 29 (iii).

Polygonum lapathifolium **L.** Willowweed. [*P. nodosum* Pers.; *P. scabrum* Moench; *P. pensylvanicum* authors, not L.]. Plants annual, erect or prostrate (rarely rooting at the nodes), 1–9 dm long; leaves petiolate to subsessile, not jointed at the base; blades 2–20 cm long, 0.6–7 cm wide, lanceolate to oblong or elliptic, acuminate to acute (abruptly rounded) apically, acute to cuneate basally, glabrous or pubescent, ciliate or glabrous marginally; stipules 5–20 mm long, not shredded, glabrous to pubescent, sparsely short-ciliate to glabrous apically; flowers several to many, borne in spikelike racemes, often aggregated in panicles, the peduncles often stipitate (or sessile) -glandular; perianth 2–3 mm long, not (or sometimes) glandular-dotted, united only near the base, 4- to 5-lobed, the lobes greenish, white, or pink, finally strongly veined, the veins branched apically and the ends recurved; styles 2 or 3; achenes lens shaped or 3-angled, brown, lustrous. Bogs, marshes, sand bars, stream and river margins at 790 to 2135 m in Cache, Daggett, Garfield, Grand, Millard, Piute, Rich, Salt Lake, San Juan, Uintah, Utah, Washington, Wayne, and Weber counties; widely scattered in North America; adventive (or indigenous in part?) from Eurasia; 43 (vi).

Polygonum minimum **Wats.** Broadleaf Knotweed. Annuals, ascending to erect, the stems not conspicuously striate, terete or triangular, 5–10 (25) cm long; leaves crowded only near the stem tips, 5–15 mm long, 2–8 mm wide, elliptic, ovate, or obovate, somewhat smaller above, acute to mucronate apically, acute basally, the blades sessile at the basal joint; stipules shredded, 2–4 mm long; flowers 1–4 axillary; pedicels included; perianth 1.5–2 mm long, united ca one-third the length, 5-lobed, the lobes greenish with white or pink edges, subequal; stigmas 3; achenes 3-angled, black, lustrous. Spruce-fir and alpine communities, often in rockstripes or talus, at ca 2745 to 3390 m in Cache, Salt Lake, and Summit counties; Alaska south to California, Nevada, and Colorado; 3 (0).

Polygonum persicaria **L.** Ladysthumb. Annuals, erect to ascending, mainly 1.5–10 dm tall; leaves petiolate to subsessile, not jointed at the base; blades 1.5–15 cm long, 0.4–4 cm wide, lanceolate to elliptic or oblong, acuminate to attenuate apically, acute to cuneate basally, with a purplish spot near the center, usually glabrous, ciliate; stipules 5–15 mm long, not shredded, usually pubescent, long-ciliate apically; flowers several to numerous, borne in terminal and usually axillary racemes; perianth 1.5–3 mm long, not glandular-dotted, united only near the base, 5-lobed, the lobes pinkish or whitish, not strongly veined and with vein ends not recurved; styles 2 or 3; achenes lens shaped or 3-angled, black, lustrous. Fence lines, canal banks, marshes, pond margins, fields, gardens, and pastures at 915 to 2135 m in Cache, Duchesne, Garfield, Salt Lake, Uintah, Utah, Wasatch, Washington, and Weber counties; widespread in North America; Eurasia; 24 (0).

Polygonum ramosissimum **Michx.** Bushy Knotweed. Annuals, ascending or erect, the stems striate and somewhat angled, 1–10 dm tall; leaves not crowded, 10–50 mm long, 2–6 mm wide, linear-oblong to lance-elliptic, usually acute, gradually reduced upward, short-petiolate above the joint; stipules shredded, 5–10 mm long; pedicels exserted; perianth 2.4–4.4 mm long, united ca one-third the length, 5-lobed, green or with pink, white, or yellow margins, the outer ones broader than the inner; stigmas 3; achenes 3-angled, brown to black, lustrous. Open sites and (mainly) in saline meadows at 1340 to 1770 m in Cache, Duchesne, Juab, Millard, Salt Lake, Uintah, and Utah counties; widespread in North America; Europe; 23 (0). The closely allied, but hardly differentiated and possibly identical *P. argyrocoleon* Steud. has been identified from Utah. The material grades continously with *P. ramosissimum*, and the older name is applied. That taxon might be valid beyond Utah.

Polygonum viviparum **L.** Alpine Bistort. Perennials, erect from short, expanded bases;

stems 7–40 (55) cm tall; basal leaves well developed, 3–25 cm long, the blades 1.5–13 cm long, 3–25 mm wide, oblong to elliptic, lanceolate, or oval, attenuate to acute apically, cuneate to subcordate basally; petioles well developed, not jointed; cauline leaves reduced upward; stipules 1–6 cm long, not shredded, often flaring and brownish apically, the upper ones seldom bladeless; flowers several to numerous, borne in terminal, spikelike racemes 2–12 cm long, at least the lower (sometimes all) replaced by bulblets; perianth 2–3.5 mm long, the lobes connate only near the base, 5-lobed, greenish with with white (cream) to pink margins, subequal; stamens often vestigial; styles 3, exserted; achenes 3-angled, brownish, lustrous, seldom developing. Sedge-grass meadows and alder-birch-willow streamside habitats, mainly in lodgepole pine and spruce-fir communities, at 2470 to 3570 m in Daggett, Duchesne, Emery, Garfield, San Juan, Sevier, Summit, and Uintah counties; Alaska east to Newfoundland, south to Oregon, Nevada, New Mexico, Minnesota, and Maine; 21 (vi).

Rumex L.

Annual, biennial, or perennial herbs from stout taproots or rhizomes; leaves alternate, basal or mostly cauline, gradually reduced upward; stipules sheathing; flowers borne in panicles, not subtended by a regular involucre; perianth of 6 (rarely 4), petaloid or sepaloid segments, the inner 3 segments enlarging in fruit and forming the "wings" or "valves" enclosing the fruit, the midveins of the valves sometimes thickened and forming grainlike tuberosities on the segments; stamens usually 6; pistil 3-carpelled, the ovary 1-loculed, 1-ovuled; styles 3; fruit a 3-angled achene.

Rechinger, K. H. Jr. 1937. The North American species of *Rumex*. Field Museum Publ. Bot. 17:1m151.

1. Flowers mostly or entirely imperfect; plants usually dioecious; leaves hastate or elliptic to oblanceolate 2

— Flowers all or mostly perfect; leaves various 3

2(1). Leaves all or some of them hastate; plants rhizomatous, sod forming, weedy .... *R. acetosella*

— Leaves elliptic, tapering at both ends; plants from thick taproots, not sod forming, not weedy .... *R. paucifolius*

3(1). Plants rhizomatous, the rhizomes black, spreading; valves of fruit mainly 10–20 mm wide .... *R. venosus*

— Plants from taproots (sometimes tuberous); valves of fruit less than 10 mm wide, or, if wider (as in *R. hymenosepalus*), from deeply set tuberous roots 4

4(3). Plants from deeply set tuberous roots; valves of fruit usually 10–20 mm wide when mature; habitats in sand dunes and other sandy sites .... *R. hymenosepalus*

— Plants from a superficial taproot; valves of fruit less than 10 mm wide at maturity; habitats various, but seldom if ever as above 5

5(4). Valves toothed along the margins, the teeth at least 1 mm long at maturity 6

— Valves entire or toothed, but, if toothed, the teeth less than 1 mm long 9

6(5). Tuberosities lacking or forming on only 1 or 2 of the valves; basal leaves mainly 5–10 cm wide or more .... *R. obtusifolius*

— Tuberosities usually forming on all valves; leaves mostly less than 4 cm wide (wider in *R. occidentalis*) 7

7(6). Plants perennial; inflorescences paniculate, not especially verticillate in lower nodes .... *R. stenophyllus*

— Plants annual; inflorescences of verticillate panicles, the verticels apparent in lower nodes and sometimes throughout 8

8(7). Valves 4–6 mm long at maturity; teeth subulate; tuberosities more than 0.5 mm wide; leaves not papillose .... *R. dentatus*

— Valves 2–3 mm long; teeth bristlelike; tuberosities less than 0.5 mm wide; leaves papillose, at least some .... *R. maritimus*

9(5). Stems with axillary branches at some or all nodes below the inflorescence, usually decumbent-ascending .... *R. salicifolius*

— Stems seldom with axillary branches below the inflorescence (except in some *R. occidentalis*), erect or essentially so 10

10(9). Valves without tuberosities, even in fruit .... *R. occidentalis*

— Valves with tuberosities on 1 or more of them 11

11(10). Valves cordate, 5–9 mm long; basal and lower leaves typically rounded to truncate or cordate, the margins not especially crisped .... *R. patentia*

— Valves triangular-ovate, mostly 3–5 mm long; basal and lower leaves rounded to acute basally, the margins strongly crisped .... *R. crispus*

Rumex acetosella **L.** Sheep Sorrel. Perennial, dioecious, erect herbs from slender rhizomes; stems 1–6 dm tall, usually unbranched below the inflorescence; basal leaves long-petiolate; cauline leaves becoming short-petiolate to subsessile; blades 1–8 cm long, 2–25 mm wide, oblong to ovate, linear, lanceolate, or elliptic, hastately lobed basally, attenuate, acute or obtuse apically; flowers numerous, imperfect, borne in leafless panicles, often purplish tinged; fruiting pedicels jointed at flower base; perianth segments 0.5–1.8 mm long in flower, the outer ones not reflexed, the inner ones enlarging and investing the achene, 1–2 mm long, ovate, entire, lacking tuberosities; achenes 1–2 mm long, yellowish brown, lustrous, sometimes adherent to the valves. Roadsides, meadows, and other open sites at 1370 to 2745 m in Beaver, Cache, Carbon, Davis, Duchesne, Emery, Grand, Piute, Salt Lake, Sanpete, Summit, Uintah, and Weber counties; widespread in North America; adventive from Eurasia; 25 (vi).

Rumex crispus **L.** Curled Dock. Perennial erect herbs from taproots; stems 3–10 dm tall or more; basal leaves long-petiolate; blades 8–40 cm long, 1.2–6 cm wide, oblong-lanceolate to elliptic, acute to rounded basally, acuminate to acute apically, undulate-crisped (the margin appearing irregularly lobed due to numerous overlapping folds in pressed specimens; cauline leaves somewhat smaller upward, short-petiolate; flowers numerous, perfect, borne in panicles with large leafy bracts to midlength or above, usually greenish; fruiting pedicels jointed above the base; perianth 1.5–2 mm long, the outer segments not reflexed; inner segments much enlarged in fruit, 3–5 mm long, cordate to deltoid or ovate, denticulate to entire, usually each (sometimes only 1 or 2) bearing a reticulately patterned tuberosity almost half as long as the segment; achenes 2–3 mm long, brown, lustrous. Weedy plants of open sites at 760 to 2440 m in probably all Utah counties; widespread in North America; adventive from Eurasia; 72 (v).

Rumex dentatus L. Annual or biennial herbs, erect, from tap or fibrous roots; stems mainly 2–7 dm tall; leaves cauline or essentially so, the lower ones long-petiolate; blades 1–6 cm long, oblong, rounded to subcordate basally, rounded to acute apically; flowers mainly perfect, borne in verticillate panicles; pedicels thickened apically, jointed below midlength; valves in fruit triangular, 4–6 mm long, toothed marginally, the teeth 1.5–2 mm long, usually all with a pronounced tuberosity. Moist, open sites at ca 1340 m in Salt Lake County (Arnow 5263 UT); adventive from Asia; 1 (0).

Rumex hymenosepalus **Torr.** Canaigre. Perennial herbs, from deeply seated, tuberous roots; stems mainly 2–10 dm tall; lower leaves long-petiolate; blades mainly 8–25 cm long, 2–12 cm wide, elliptic to lanceolate or oblanceolate, cuneate basally, acute to acuminate apically, more or less fleshy; cauline leaves reduced and short-petiolate upward; stipular sheathes 1–4 cm long; panicles compact, 10–35 (40) cm long, usually pinkish; pedicels 4–12 mm long, jointed near the middle; perianth 2–4 mm long at anthesis, the valves 8–18 mm long in fruit, cordate-ovate to suborbicular, reticulate, rounded apically. Blackbrush, Vanclevea, ephedra, and other sandy desert shrub communities at 760 to 1680 m in Daggett, Garfield, Grand, Kane, San Juan, Uintah, and Washington counties; California, Nevada, Arizona, New Mexico, Texas, Colorado, and Wyoming; Mexico; 49 (vi).

Rumex maritimus **L.** Golden Dock. [*R. maritimus* var. *athrix* St. John, type from Vermillion]. Annual (or biennial?) herbs, erect from taproots; stems 0.5–8 dm tall; basal leaves usually reduced; cauline leaves well developed, but reduced in size upward, short-petiolate; blades 2–15 cm long, 1–4 cm wide, oblong to lanceolate, rounded to subcordate or acute basally, acute to acuminate or obtuse apically, undulate to plane; flowers numerous, borne in compact axillary clusters, the inflorescence leafy throughout or nearly so, often half the total plant height, greenish; pedicels jointed near or at the base; perianth 1–2 mm long in flower, the outer ones not reflexed; inner segments 3–7 mm long (including the acuminate apex) in fruit, ovate, with 2–4 slender teeth per segment, each tooth 1.5–5 mm long, the valves each usually with a well-developed tuberosity ca half as long as the segment; achenes 1.5–2 mm long, brown, lustrous. Lake shores, stream margins, pond and seep margins, and other moist sites at 1220 to 2565 m in Cache, Carbon, Daggett, Duchesne, Emery, Garfield, Juab, Kane, Piute, Rich, Salt Lake, Sanpete, Uintah, and Wayne counties; widespread in North and South America; Europe; 40 (ii). Our specimens belong to var. fuegineus (Phil.) Dusen [*R. fuegineus* Phil.; *P. maritimus* ssp.*fuegineus* (Phil.) Hulten].

Rumex obtusifolius **L.** Bitter Dock. Perennial, erect herbs from taproots; stems 4–12 dm tall (or more), usually unbranched below the inflorescence; basal leaves long-petioled; blades 10–40 cm long, 4–15 cm wide, ovate to oblong or lanceolate, cordate to truncate basally, obtuse to acute or acuminate apically, undulate; cauline leaves like the basal ones, somewhat smaller and with shorter petioles upward; flowers numerous, perfect, borne in panicles with leafy bracts to the middle or above, usually greenish; perianth segments 2–3 mm long, the outer ones not reflexed; inner segments 3.5–5 mm long in fruit, ovate, with 4–6 teeth per segment, each tooth 0.5–2 mm long, at least some valves with a prominent tuberosity; achenes 1.5–2 mm long, brown, lustrous. Rural weeds, mainly on canal and stream banks, at 1370 to 2290 m Cache, Davis, Salt Lake, Tooele, and Utah counties; widespread in North America; adventive from Eurasia; 13 (i).

Rumex occidentalis **Wats.** Western Dock. [*R. subalpina* Jones, type from near Marysvale]. Perennial, erect herbs from taproots; stems 5–20 dm tall, usually unbranched below the inflorescence, often reddish tinged; basal leaves long-petioled; blades 0.6–4 dm long, 3–15 cm wide, oblong to ovate or oblong-lanceolate, cordate to truncate or obtuse basally, rounded to obtuse or acute apically, usually more or less undulate-crisped; cauline leaves reduced upward; flowers numerous, perfect, borne in panicles with leafy bracts only near the base, greenish; fruiting pedicels obscurely jointed near or below the middle; perianth segments 2–4 mm long, the outer ones not reflexed, the inner ones 4–10 mm long in fruit, ovate to oval (mostly longer than broad), denticulate to entire, lacking tuberosities; achenes 3–4 mm long, brown, lustrous. Meadows, aspen, and spruce-fir communities at 1830 to 3175 m in Duchesne, Garfield, Sanpete, and Wasatch counties; Alaska to Quebec, south to California, evada, New Mexico, and South Dakota; 5 (0).

Rumex patentia **L.** Perennial, erect herbs from a taproot; stems mainly 6–15 dm tall, unbranched below inflorescence; basal leaves long-petiolate; blades mainly 10–30 cm long and 6–15 cm wide, ovate-oblong to lanceolate or oblong, subcordate to truncate or acute basally, acute to acuminate apically; panicles dense, 2–5 dm long, leafy bracteate to the middle; pedicels jointed at or below the middle; flowers perfect, outer segments 1.5–2 mm long, finally reflexed, inner ones 5–9 mm long in fruit, ovate to suborbicular and cordate basally, entire to denticulate, one valve (only) with a tuberosity; achenes 3–3.5 mm long. Weedy species of open sites at 1340 to 2440 m in Cache, Salt Lake, and Utah counties; widely distributed in North America; introduced from Eurasia; 6 (i). This species is not clearly differentiated from

R. occidentalis q.v., and evidently forms intermediates with both *R. crispus* and *R. obtusifolius*.

Rumex paucifolius **Nutt.** Alpine Sorrel. Perennial, dioecious herbs from a taproot and thick root-crown; stems mainly 1–7 dm tall, unbranched below the inflorescence; basal leaves well developed, petiolate; blades 2–13 cm long, elliptic, acute to attenuate at both ends, much reduced upward; inflorescence essentially ebracteate, often as much as half the plant height; flowers imperfect, commonly red; pedicels jointed near the middle; outer perianth segments not reflexed; valves 3–4 mm long, cordate to suborbicular, lacking tuberosities; achenes smooth, ca 1.5 mm long. Meadows in aspen and spruce-fir communities at 2095 to 3050 m in Cache, Rich, Salt Lake, Summit, and Wasatch counties; British Columbia and Alberta, south to California and Colorado; 23 (i).

Rumex salicifolius **Weinm.** Beach Dock. Perennial, decumbent to ascending (or erect) herbs from taproots, mainly 2–6 dm tall, branching from the lower nodes; leaves mostly cauline, short-petiolate, not much reduced upward; blades 3–20 cm long, 3–30 mm wide, narrowly lanceolate to oblong or linear, acute to rounded basally, acute apically, plane to undulate, not crisped; flowers numerous, perfect, borne in panicles, these more or less leafy-bracteate, usually greenish; fruiting pedicels jointed near the base; perianth segments 1–2 mm long, outer ones not reflexed, inner 2–4 mm long in fruit, ovate to deltoid, entire to denticulate, with tuberosities on all valves or lacking on all valves; achenes 1.5–2.5 mm long, brown, lustrous. Salt grass, salt desert shrub, sagebrush, pinyon-juniper, mountain brush, aspen-tall forb, Douglas fir, and spruce-fir communities at 1340 to 3205 m in Beaver, Cache, Carbon, Davis, Duchesne, Emery, Garfield, Iron, Juab, Kane, Piute, Rich, Salt Lake, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Weber counties; Alaska to Quebec, south to California, Texas, and New York; 79 (viii). Our material has been treated within two varities; var. ***montigenitus*** **Jepson,** with tuberosities lacking on the valves, and var. ***mexicanus*** **(Meisn.) C. L. Hitchc.** [*R. mexicanus* Meisn.; *R. utahensis* Rech. f.], with tuberosities on the valves. Transitional specimens connect the varieties, which are not geographically correlated. Both of the varieties are regarded as phases within ssp. *triangulivalvis* Danser.

Rumex stenophyllus **Ledeb.** Perennial, erect herbs from taproots, mainly 3–9 dm tall; leaves basal and cauline, petiolate; blades 4–20 cm long, 1–5 cm wide, lanceolate to lance-oblong or elliptic, obtuse to acute basally, acute to attenuate apically; panicles loose to dense, mainly 2–4 dm long; pedicels jointed below the middle; outer perianth segments 1–2 mm long, the valves with tuberosities; achenes 2–2.5 mm long, lustrous. Palustrine, riparian, and lacustrine habitats at ca 1400 to 1590 m in Uintah (near Ouray) County; Wyoming; adventive from Eurasia (?); 5 (0). These plants are more or less intermediate between *R. obtusifolius* and *R. crispus*, neither of which is known from the locality where this species occurs.

Rumex venosus **Pursh** Perennial herbs from creeping rhizomes; stems erect, 1–5 dm tall, usually branched; stipules conspicuous, 1–5 cm long; leaves cauline, the lowermost lacking blades; blades mostly 2–14 cm long, 1–6 cm wide, ovate to elliptic or oblong, leathery, obtuse to acute basally; flowers numerous, in more or less leafy bractrate panicles; pedicels jointed near the middle; perianth segments 4–5 mm long, the valves 15–35 mm long, usually suffused with red, orbicular to subreniform, cordate basally, rounded apically, reticulate, lacking tuberosities; achenes 5–6 mm long, smooth. Sand dunes and other sandy habitats at 1370 to 2230 m in Cache, Davis, Grand, Juab, Kane, Millard, Salt Lake, Tooele, Uintah, and Utah counties; British Columbia to Saskatchewan, south to California, New Mexico, and Nebraska; 15 (iii).

SOIL WATER AND TEMPERATURE RESPONSE TO PRESCRIBED BURNING[1]

S. G. Whisenant[2], C. J. Scifres[3], and D. N. Ueckert[4]

Abstract.— Prescribed burning of Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.) communities reduced soil water contents for two to six months, and additional reductions occurred when the subsequent crop of cool-season grasses and forbs began growth. These soil water reductions occurred despite reduced plant production following burning. Soil water reductions were greater at 15 to 45 cm depths than in the upper 15 cm and greater following spring burning. Soil temperatures were higher on burned plots for most of the first year following burning.

Fire can affect soil through: (1) direct action of heat, (2) removal of mulch and standing crop, and (3) the redistribution of certain nutrients. Grassland fires are flashy and seldom create prolonged high temperatures at the soil surface (Daubenmire 1968, Vogl 1974, Wright and Bailey 1982). Thus, it is unlikely that the direct action of heat has a significant effect on grassland soils. Although changes in soil temperatures during grassland fires are relatively small, soil temperatures may be increased following the fire due to increased solar insolation. Sharrow and Wright (1977) reported increased soil temperature at 8 cm depths for 15–45 days following burning of tobosagrass [*Hilaria mutica* (Buckl.) Benth.] on a Stamford clay site. Since the same change occurred on similar areas from which top growth and mulch were mechanically removed, soil insulation by mulch was apparently responsible for lower soil temperatures on unburned areas.

In most arid and semiarid grasslands, soil water content is the single most important factor influencing primary production (Webb et al. 1978). Fire is a natural phenomenon of most grassland ecosystems and can profoundly affect soil water levels (Daubenmire 1968). Following burning of grasslands, infiltration has been reported as both reduced (Hanks and Anderson 1957) and unaffected (Ueckert et al. 1979). Changes in infiltration rates of rangeland soils are usually attributed to litter removal rather than direct heat effects (Daubenmire 1968).

One innovative study (Sharrow and Wright 1977) found soil water levels were reduced in the 0–8 cm depths following litter removal on soil with active roots. However, when active roots were excluded litter removal did not reduce soil water levels. They concluded that "reduced soil moisture on burned areas is primarily due to increased transpirational water use by the rapidly growing plants rather than evaporation of water from bare soil." A long-term study of soil water trends following burning at Kansas Flint Hill bluestem ranges concluded that soil water reductions were greater following early burning and in the deeper soil levels (Anderson 1965).

The research data, to date, describes soil water and soil temperature changes occurring following burning of warm-season grasslands such as tobosagrass and big bluestem (*Andropogon gerardii* Vitman). Little information is available on changes in soil water and soil temperature following burning of a predominantly cool-season grassland. The objectives of this study were to evaluate the influence of fall, winter, and spring burning on soil water contents and soil temperatures in a Texas wintergrass (*Stipa leucotricha* Trin. & Rupr.) community.

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STUDY AREAS AND METHODS

Research was conducted on a 6.5 ha study area in McCulloch County, Texas. This area typically has dry winters and hot summers, with precipitation peaks in April–May, and September–October. The mean annual precipitation is 59 cm (Bynum and Coker 1974).

Tobosa clay (fine, montmorillonitic, thermic, Typic Chromustert) soils occur on the lower areas of the study site, and Valera clay soils (fine, montmorillonitic, thermic, Petrocalcic Calcuistoll) occur on the uplands. The Tobosa clay is deep, moderately well drained, and cracks deeply when dry. Water enters the dry, cracked soil very rapidly, but water movement into wet soil is extremely slow. Runoff is medium and the available water storage capacity is high (Bynum and Coker 1974). The Valera clay is moderately deep and well drained, with moderately slow permeability. Surface runoff is slow to medium and available-water capacity is high (Bynum and Coker 1974).

Treatments were applied to 0.3 ha plots arranged as a randomized complete block experiment, with two replications. Treatments were: unburned, September 1979 burn, January 1980 burn, March 1980 burn, and November 1980 burn. Soil water contents were determined gravimetrically (Gardner 1965) on five soil samples each from 0 to 15, 15 to 30, and 30 to 45 cm depths from each replication. Soil water samples were collected monthly from November 1979 to April 1981 and oven dried at 100 C for 48 hr. Soil temperatures at 3, 15, and 30 cm below the surface were determined on burned and unburned plots using five placements of a probe-type dial thermometer. Temperature data were collected at midday at approximately 30-day intervals from September 1979 to March 1981.

Soil water data were subjected to analyses of variance using plot means. Treatment means were tested for significant differences with Duncan's multiple range test ($P \leq 0.05$) where appropriate.

RESULTS AND DISCUSSION

SOIL WATER CONTENT: Burning in September 1979 reduced soil water contents in the 0 to 15 cm depth zone for the first three months following burning (Table 1). Plots burned in March 1980 contained less soil water in the surface 15 cm zone in June 1980 than did unburned plots. Decreases in soil water contents of burned plots coincided with initiation of growth of Texas wintergrass and several cool-season, annual grasses and forbs (*Limnodea arkansana*, *Bromus japonicus*, and *Xanthocephalum dracunculoides*). A similar pattern was observed at another study area in Coleman County (Whisenant 1982).

Soil water contents at 15 to 30 and 30 to 45 cm depths followed similar trends to that of the surface 15 cm (Table 1). Soil water was reduced for two to six months following burning and again when the next season's cool-season grasses and forbs began growth. The greatest reductions in soil water contents occurred following March burns.

These data differ in some respects from studies of postburn soil water contents in rangelands dominated by warm-season grasses (Anderson 1975, Sharrow and Wright 1977). In this study, soil water reductions were greater following the later burns rather than the earlier burns as reported by Anderson (1965). Probably the most distinct difference was the reduction in soil water contents when the cool-season grasses initiated growth the following season. This trend was not apparent in studies of postburn soil water in rangelands dominated by warm-season grasses (Anderson 1965, Sharrow and Wright 1977). As in previous studies, soil water contents were depleted more at greater depths following burning.

Other researchers have reported that decreased soil water contents following burning were accounted for by increases in plant production and transpiration (Sharrow and Wright 1977). However, soil water on this study site was reduced despite greatly reduced primary production on the burned plots (Whisenant et al. 1984). This study area was on a concave site with a deep soil that cracked when dry, had little slope, and contained gilgai relief. Thus, it is unlikely that runoff was an important factor. Therefore, reduction in soil water content might be attributed to increases in transpiration from the remaining plants and greater evaporational

TABLE 1. Mean soil water contents (%) at 0 to 15, 15 to 30, and 30 to 45 cm depths at monthly intervals following burning on four dates in 1979–1980 in McCulloch County, Texas.[1]

		Date burned			
Date	Unburned	September 1979	January 1980	March 1980	November 1980
			0 to 15 cm		
Nov 1979	11a	8 b	–	–	–
Dec 1979	31a	29 b	–	–	–
Jan 1980	29a	29a	–	–	–
Feb 1980	32a	32a	29 b	–	–
Mar 1980	28a	28a	27a	–	–
Apr 1980	22ab	23a	19 b	21ab	–
May 1980	21a	23a	22a	20a	–
Jun 1980	16a	16a	15ab	14 b	–
Jul 1980	12a	11a	12a	11a	–
Aug 1980	11a	10a	11a	10a	–
Sep 1980	35a	36a	36a	33 b	–
Oct 1980	33a	32ab	31ab	31 b	–
Nov 1980	27a	24 b	24 b	23 b	–
Dec 1980	33a	33a	31a	30 b	30 b
Jan 1981	37a	32 b	35a	36 b	29 c
Feb 1981	31a	29ab	28ab	27 b	26 b
Mar 1981	33a	34a	31a	30a	30a
Apr 1981	30a	30a	29a	29a	27 b
			15 to 30 cm		
Nov 1979	11a	9 b	–	–	–
Dec 1979	30a	27 b	–	–	–
Jan 1980	29a	27 b	–	–	–
Feb 1980	31a	28 b	27 b	–	–
Mar 1980	25a	22 b	22 b	–	–
Apr 1980	24a	21 b	21 b	20 b	–
May 1980	18ab	18ab	20a	16 b	–
Jun 1980	17a	16ab	15 b	13 c	–
Jul 1980	15a	13 b	16a	13 b	–
Aug 1980	13a	12ab	12ab	11 b	–
Sep 1980	32a	32a	31a	26 b	–
Oct 1980	32a	31a	31a	30a	–
Nov 1980	29a	27a	27a	27a	–
Dec 1980	32a	32a	31a	29 b	29 b
Jan 1981	36a	31 b	32 b	30 bc	29 c
Feb 1981	30a	27 b	26 b	27 b	27 b
Mar 1981	32a	32a	32a	31a	29 b
Apr 1981	31a	31a	30a	30a	28 b
			30 to 45 cm		
Nov 1979	12a	8 b	–	–	–
Dec 1979	29a	27 b	–	–	–
Jan 1980	29a	26 b	–	–	–
Feb 1980	30a	27 b	25 b	–	–
Mar 1980	24a	24a	21 b	–	–
Apr 1980	20ab	23a	21ab	19 b	–
May 1980	18a	18a	18a	15 b	–
Jun 1980	17a	16a	15 b	14 c	–
Jul 1980	15ab	14 bc	16a	13 c	–
Aug 1980	14a	13ab	13a	12 b	–
Sep 1980	32a	31a	31a	30 b	–
Oct 1980	31a	31ab	31ab	28 b	–
Nov 1980	28a	28a	28a	27a	–
Dec 1980	31a	27 b	26 b	29a	28 b
Jan 1981	32a	29 b	28 b	29 c	28 c
Feb 1981	32a	29 b	29 b	25 c	26 bc
Mar 1981	35a	34a	31a	29 b	27 b
Apr 1981	31a	30a	29a	28a	27 b

[1] Means within a row followed by the same letter are not significantly different ($P \leq 0.05$) according to Duncan's multiple range test.

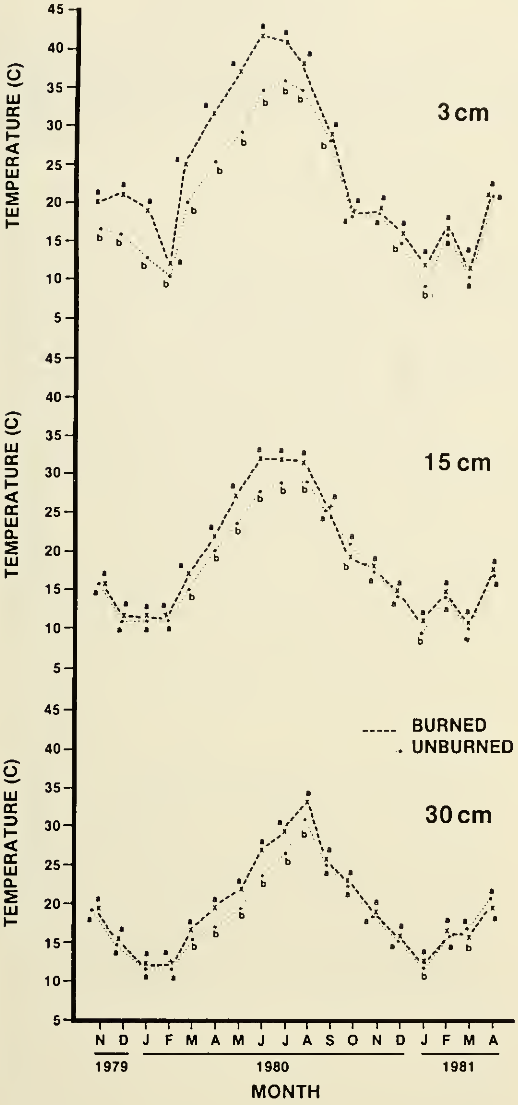

Fig. 1. Soil temperature (C) at 3 cm (top), 15 cm (middle), and 30 cm (bottom) at monthly intervals following burning in September 1979 in McCulloch County, Texas. Points within a depth and month followed by the same letter are not significantly different (P≤0.05) according to Duncan's multiple range test.

losses from the soil. Unburned plots contained 3 to 5 cm of ground mulch in addition to standing litter. Burning removed essentially all the ground mulch and standing litter, which should have increased the vapor pressure gradient between the soil surface and atmosphere. The high clay percentage (44%) of this soil would greatly facilitate capillary movement of soil water to the surface from lower soil layers. Reductions in soil water contents were greater at 15 to 30 and 30 to 45 cm depths than in the surface 15 cm, perhaps because the lower soil layers received little or no additions of water from the light rains of late spring and summer. Eliminating the standing litter created a more xeric micro-environment for the remaining plants, which could have increased transpiration rates of plants on burned relative to unburned areas.

SOIL TEMPERATURE: Burning affects postburn soil temperatures indirectly by removing living vegetation and mulch. A consequence of this reduction in ground cover is greatly increased solar insolation on the soil surface.

Soil temperatures at 3 cm depths were greater on the burned plots for the first 11 months after the September 1979 fires (Fig. 1). Soil temperatures at 3 cm on burned plots did not differ significantly from those of unburned plots in October and November 1980. Temperatures on burned plots in December 1980 and January 1981 were again greater than on the unburned plots. Surface temperatures equilibrated between the two treatments by February 1981 (16 months postburn).

Soil temperatures at 15 cm changed more slowly following burning than did temperatures at the surface (Fig. 1). The first significant soil temperature differences at 15 and 30 cm were not detected until 5 months postburn (March 1980). At that time, soil temperatures on burned plots were significantly higher than on unburned plots. Soil temperatures at 15 and 30 cm remained higher on burned than unburned plots until September 1980 (11 months postburn). Soil temperatures at 15 and 30 cm on burned plots appeared to equilibrate with unburned plots after 11 months. In general, soil temperatures were higher on burned plots for most of the first year following burning.

CONCLUSIONS

This research describes a somewhat different postburn soil water response in a cool-season grass-dominated rangeland than has been reported in warm-season grass-dominated rangelands. Several hypotheses are proposed that may explain the observed soil water change. Soil water contents were reduced for two to six months following burning and again when the next crop of cool-season grasses and forbs began growth. In contrast to other studies where reductions in soil water were accompanied by and attributed to increased plant production, soil water contents and net primary production were reduced by burning in this experiment. The reductions in soil water contents following burning were possibly a result of increased evaporation from the soil and greater transpiration from the remaining plants. Soil water reductions were greater at 15 to 45 cm than in the upper 15 cm, presumably because the deeper soil layers were in the zone of greatest root activity and received little or no water from the relatively light late spring and summer rains. In addition, capillary flow, caused by evaporation from the soil, may have depleted lower soil layers of water while increasing soil water in the upper layer.

Soil temperatures were increased on burned plots for most of the first year following burning compared to adjacent, unburned rangeland. Fire indirectly affected postburn soil temperature through removal of living vegetation and litter, which increased solar radiation on the soil surface, thus increasing soil temperatures.

LITERATURE CITED

ANDERSON, K. L. 1965. Time of burning as it affects soil moisture in an ordinary upland bluestem prairie in the Flint Hills. J. Range Manage. 18:311–316.

BYNUM, O. W., AND J. L. COKER. 1974. Soil survey of McCulloch County, Texas. U.S. Dept. Agric., Soil Conserv. Ser. 91 p.

DAUBENMIRE, R. 1968. Ecology of fire in grasslands. Advan. Ecol. Res. 5:207–266.

GARDNER, W. H. 1965. Water Content. Pages 82–125 *in* C. A. Black, ed., Methods of soil analysis, Part I. Amer. Soc. Agron. Madison, Wisc.

HANKS, R. J., AND K. L. ANDERSON. 1957. Pasture burning and moisture conservation. J. Soil and Water Conserv. 12:228–229.

NEUENSCHWANDER, L. F., H. A. WRIGHT, AND S. C. BUNTING. 1978. The effect of fire on a tobosagrass-mesquite community in the Rolling Plains of Texas. Southwest Nat. 23:315–338.

SHARROW, S. H., AND H. A. WRIGHT. 1977. Effects of fire, ash, and litter on soil nitrate, temperature, moisture and tobosagrass production in the rolling plains. J. Range Manage. 30:266–270.

UECKERT, D. N., T. L. WHIGHAM, AND B. M. SPEARS. 1978. Effects of burning on infiltration, sediment, and other soil properties in a mesquite-tobosagrass community. J. Range Manage. 31:420–425.

VOGL, R. J. 1974. Effects of fire on grasslands. Pages 139–149 *in* T. T. Kozlowski, ed., Fire and Ecosystems. Academic Press, New York.

WEBB, W., S. SZAREK, W. LAURENROTH, R. KINERSON, AND M. SMITH. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. Ecology 59:1239–1247.

WHISENANT, S. G. 1982. Ecological effects of fire on Texas wintergrass (*Stipa leucotricha*) Communities. Unpublished dissertation. Texas A & M Univ., College Station. 110 pp.

WHISENANT, S. G., D. N. UECKERT, AND C. J. SCIFRES. 1984. Effects of fire on Texas wintergrass communities. J. Range Manage. 35:387–391.

WRIGHT, H. A., AND A. W. BAILEY. 1982. Fire ecology. John Wiley and Sons, New York. 501 pp.

HABITAT AND DISTRIBUTION OF PYGMY RABBITS (*SYLVILAGUS IDAHOENSIS*) IN OREGON

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ABSTRACT.— An investigation to determine the location and extent of populations of pygmy rabbits (*Sylvilagus idahoensis*) in Oregon, and to describe several biotic and physical components within communities that include pygmy rabbits, was conducted from October 1981 to September 1983. Of 211 sites suspected of supporting the species based on interpretation of museum records, aerial photographs, soil maps, and interviews with biologists and area residents, 51 exhibited evidence of being inhabited when examined in summer 1982. Soil and vegetation components were sampled at 15 sites occupied by pygmy rabbits and 21 sites adjacent thereto. At inhabited sites, mean soil depth (51.0 ± 2.3 cm), mean soil strength of surface (0.8 ± 0.2 kg/cm^2) and subsurface (3.8 ± 0.3 kg/cm^2) horizons, shrub height (84.4 ± 5.8 cm), and shrub cover (28.8 ± 1.4%) were significantly greater ($P < 0.05$) than at unoccupied adjacent sites, but percent basal area of perennial grasses (3.7 ± 0.9%), density of annual grasses (5.2 ± 2.1/1,000 cm^2), density of forbs (3.4 ± 0.6/1,000 cm^2), and cryptogam cover (2.4 ± 0.5%) were not. Except for the clay component of subsurface soils, texture of surface and subsurface soils were not significantly different between sites occupied by pygmy rabbits and adjacent sites. The affinity of pygmy rabbits for areas with greater shrub cover, shrub height, soil strength, and soil depth, and, to a small degree, coarser soil texture possibly was related to availability of forage, security from predation, and ease of burrow construction. Analysis of 472 samples of sagebrush (*Artemisia tridentata*) collected at and near sites inhabited by pygmy rabbits indicated their distribution was not dependent upon the presence of specific subspecies of sagebrush. A marked decrese in evidence of occupancy of sample sites and of pygmy rabbit activity at occupied sites in 1983 indicated that populations of pygmy rabbits were susceptible to rapid declines and possible local extirpation. Fragmentation of sagebrush communities poses a potential threat to populations of pygmy rabbits, but the severity of the threat presently is unknown.

Pygmy rabbits (*Sylvilagus idahoensis*), the smallest leporid, are endemic to the Great Basin and adjacent intermountain areas of the western United States (Green and Flinders 1980a). The distribution of this species is disjunct within a geographic range that reaches its westernmost extent in Oregon (Hall 1981). In Oregon pygmy rabbits occur in seven counties south and west of the approximate line connecting Klamath Falls, Fremont, Redmond, and Baker (Olterman and Verts 1972). These rabbits typically are associated with clumped stands of big sagebrush (*Artemisia tridentata*) (Anthony 1913, Davis 1939, Orr 1940, Bradfield 1975), where soils usually are deep and friable (Orr 1940, Janson 1946, Campbell et al. 1982). Where habitat requirements are met, pygmy rabbits dig relatively shallow burrows, usually in aggregations (Janson 1946). Because *S. idahoensis* is the only native leporid to excavate its own burrows (Janson 1946), the influence of soil characteristics upon its distribution likely is unique among rabbits and hares of this continent. Associations between pygmy rabbits and habitat types, however, are based primarily on natural histories; quantitative descriptions of soil characteristics at sites occupied by pygmy rabbits do not exist, and quantitative descriptions of vegetation components at sites inhabited by pygmy rabbits are known from a single study conducted in Idaho (Green and Flinders 1980b). Because large areas of sagebrush land are undergoing renovation for grazing or conversion to irrigated agriculture (Green and Flinders 1980b), and because the current status of pygmy rabbits in Oregon is undetermined (Olterman and Verts 1972), information regarding habitats occupied by *S. idahoensis* should be of special interest to biologists and managers. The objectives of this study were to determine the location and extent of populations of pygmy rabbits in Oregon, and to describe several biotic and physical components of habitats occupied by pygmy rabbits.

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METHODS

Location of Areas Occupied by Pygmy Rabbits

The search for pygmy rabbits was conducted in areas where pygmy rabbits were collected previously. Olterman and Verts (1972) reported that museum collections contained S. *idahoensis* from 37 sites in Oregon (Fig. 1A), but locality descriptions obtained from these records lacked precision needed to locate populations. Interpretation of aerial photographs and information obtained from soil maps were used to narrow the search for pygmy rabbits within general areas identified from locality descriptions for museum records. In cooperation with the Environmental Remote Sensing Applications Laboratory at Oregon State University, stereoscopic surveys of U-2 high-altitude infrared photographs were used to locate areas most likely to support the species. Locations of areas with photographic characteristics similar to sites with known populations of pygmy rabbits were recorded on U.S. Geographic Survey 1:250,000 topographic maps. Soil maps and soil descriptions (Oregon Water Resource Board 1969) were used to identify deep, friable, sandy-loam soils in southern and eastern Oregon. Correspondence and interviews with biologists and field personnel from state and federal agencies and local residents provided locations of known or suspected areas occupied by pygmy rabbits; these areas also were examined.

The search for sites occupied by pygmy rabbits was conducted from June to October 1982. Two people on foot searched for evidence of pygmy rabbits at each site for approximately 30 min; areas inhabited by pygmy rabbits were identified by presence of burrows and fecal pellets or by sighting of individuals. Distribution, degree of weathering, and abundance of fecal pellets provided a basis for distinguishing burrows used by pygmy rabbits and were an aid in estimating the limits of sites occupied by the species. We considered a pygmy rabbit burrow to include all burrow entrances associated with it.

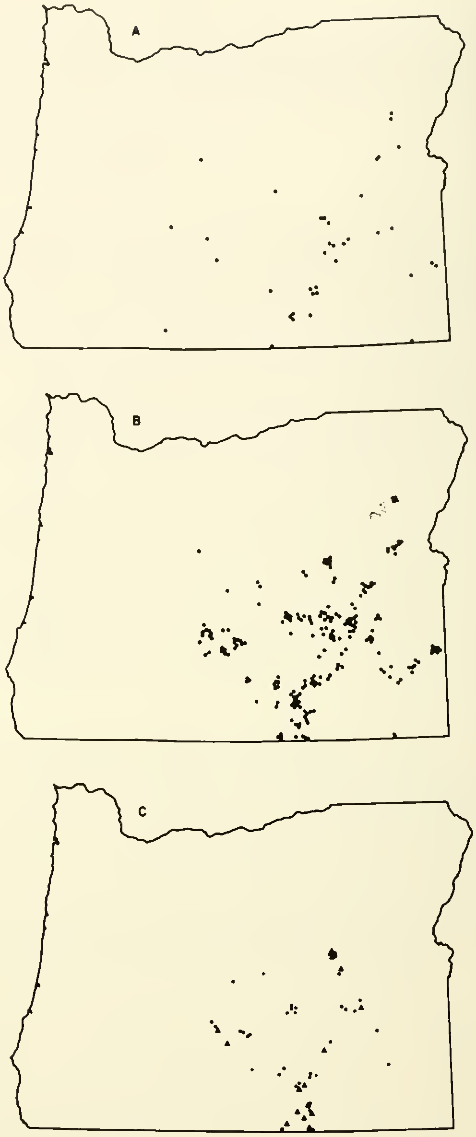

Fig. 1. A. Thirty-seven sites at which museum specimens of pygmy rabbits were collected in Oregon. (Map modified after Olterman and Verts [1972]. One map location without accompanying record of locality was deleted.) B. Two hundred eleven sites examined for evidence of pygmy rabbits, Oregon, 1982. C. Fifty-one sites at which evidence of occupancy by pygmy rabbits was found, Oregon, 1982. Triangles indicate those sites at which soil and vegetation were sampled; circles indicate those sites that did not meet criteria for sampling.

Sites at which pygmy rabbits occurred and at which habitats were sampled in 1982 were examined during summer 1983 to ascertain continued use by pygmy rabbits. Presence of open burrows and recently deposited fecal pellets were criteria used to establish continued occupancy of sites.

Sampling of Soil and Vegetation

Biotic and physical properties of sites inhabited by pygmy rabbits were sampled from July to October 1982. Sampling was conducted at a site if evidence of recent activity of S. *idahoensis* was observed and four or more burrows occurred with a maximum distance of 200 m between burrows.

Three parallel line-transects 30 m long and 10 m apart were established at randomly selected starting points at each site sampled. At one site (site 12), sampling was repeated because of apparent vegetative heterogeneity. Transects were located parallel to contours of slopes when present. Shrub height and shrub cover were measured along line transects (Pieper 1978), and clippings from all *Artemisia tridentata* plants that intercepted the transects were collected. Ten 20 by 50 cm plots were placed uniformly along each transect to estimate basal areas of perennial grasses, densities of annual grasses and forbs, and cryptogam cover (Daubenmier 1959). Soil samples were collected at the surface and at 40 cm below the surface (soil depth permitting) at five uniformly spaced stations along each transect; samples from a common depth were combined to obtain a single sample for each transect. Soil depth to 60 cm was recorded and soil strength at the surface and at 40 cm below the surface (soil depth permitting) was measured at each of the five stations with a Soil Test Model CL-700 pocket penetrometer. When soil strength exceeded the limits of the penetrometer, 5.0 kg/cm², the maximum value was recorded. A clinometer was used to measure ground slope in the immediate vicinity of each rabbit burrow, and the number of entrances to each burrow system was recorded.

Procedures for sampling soil and vegetative characteristics at sites occupied by pygmy rabbits were repeated at adjacent shrub communities where pygmy rabbit burrows were not found. The sampling of adjacent shrub communities was restricted to areas less than 100 m from a peripheral pygmy rabbit burrow. Pygmy rabbits were presumed to have had access to these sites because S. *idahoensis* reportedly traveled 100 m or more from their burrows in winter and summer (Bradfield 1975, Wilde et al. 1976). Because pygmy rabbit burrows often were distributed along the contours of slopes, adjacent shrub communities were sampled above and below sites occupied by the species. Adjacent communities were not sampled if the shrub component was absent or if evidence of recent habitat disturbance was detected.

Soil texture (Bouyoucos 1962) and subspecific identity of *A. tridentata* were determined (Winward and Tisdale 1969, Shumar et al. 1982) upon return of samples to Oregon State University. Alcohol-leaf extracts from five randomly selected samples of *A. tridentata* from those collected along each transect were examined under long-wave ultraviolet light for blue fluorescence to identify *A. t. vaseyana*. Spectrophotometric analysis of remaining extracts was used to separate *A. t. wyomingensis* from *A. t. tridentata*.

Two-tailed paired t tests were used to determine the probability that mean differences of the same habitat variables sampled at sites occupied by pygmy rabbits and adjacent sites were greater than zero. For sites occupied by pygmy rabbits at which more than one adjacent site was sampled, data from adjacent sites were averaged for analysis. Square-root transformations were performed on all variables measured as percents, but, because inferences drawn from analysis of transformed and nontransformed data did not differ, nontransformed data are reported herein. Discriminant analysis (Klecka 1975) was used to identify habitat components that best distinguished sites occupied by pygmy rabbits from adjacent sites. Habitat variables used in discriminant analysis were shrub cover, shrub height, surface and subsurface soils strengths, soil depth, percent basal area of perennial grasses, density of annual grasses, density of forbs, and percent sand in surface and subsurface soils. Interpretation of the discriminant function was based on pooled within-group correlations between the canonical discriminant function and habitat variables. Pearson correlation coefficients were calculated for habitat variables measured at all sites. Stepwise-multiple regression was used to examine the relationship among number of burrow entrances and soil variables measured at inhabited sites. For all statistical analyses, we accepted $P < 0.05$ as being significant.

RESULTS

Evidence of pygmy rabbits was observed at 51 of 211 sites examined (Figs. 1B and 1C). Fifteen areas occupied by pygmy rabbits met criteria for sampling (Table 1). Twenty-one areas adjacent to 13 sites occupied by pygmy rabbits also were sampled.

Shrub height, shrub cover, and soil depth were significantly greater at 13 sites occupied by pygmy rabbits than at 21 adjacent sites (Table 2). In contrast, percent basal area of perennial grasses, density of annual grasses, density of forbs, and cryptogam cover were not significantly different between occupied and adjacent sites. Soil strengths at surface and subsurface horizons were significantly less at sites occupied by pygmy rabbits than at adjacent sites (Table 2). With exception of percent clay for subsurface soils, components of soil texture were not significantly different at occupied and adjacent sites (Table 2).

Green and Flinders (1980b) also reported shrub height and shrub cover at six sites inhabited by pygmy rabbits in Idaho were significantly greater than in areas that represented 30 small rodent, yellow-bellied marmot (*Marmota flaviventris*), and Uinta ground squirrel (*Spermophilus armatus*) habi-

TABLE 1. Legal description, elevation, ownership, and description of burrows at 15 sites occupied by pygmy rabbits at which characteristics of soil and vegetation were sampled, Oregon, 1892.

Site number	County	Location*	Elevation (m)	Ownership or managing agency	Number burrows	$\bar{X}$ number entrances/ burrow	$\bar{X}$ slope at burrows (%)
1	Lake	T38S, R28E, sec. 34	1585	Private	16	2.3	5.1
2	Lake	T37S, R28E, sec. 14 & 15	1675	Bureau of Land Management	10	1.3	1.5
3	Lake	T39S, R27E, sec. 2	1570	National Wildlife Refuge	7	2.6	3.4
4	Lake	T40S, R27E, sec. 36	1500	State of Oregon	8	2.6	1.2
5**	Lake	T39S, R25E, sec. 33	1400	Bureau of Land Management	7	1.4	7.4
6**	Lake	T35S, R26E, sec. 28	1830	National Wildlife Refuge	9	1.9	16.5
7**	Lake	T34S, R26E, sec. 36	1615	National Wildlife Refuge	5	1.7	5.0
8**	Lake	T38S, R26E, sec. 9	1830	Private	7	1.0	12.3
9**	Lake	T28S, R15E, sec. 22	1380	Bureau of Land Management and Private	12	2.3	2.4
10**	Lake	T26S, R14E, sec. 22	1325	Bureau of Land Management	9	3.9	4.0
11**	Harney	T29S, R29½E, sec. 26	1540	Bureau of Land Management	5	1.6	0.0
12	Harney	T24S, R34E, sec. 18	1280	Private	8	1.9	0.0
13**	Grant	T18S, R32E, sec. 29	1385	Bureau of Land Management	5	1.4	13.0
14**	Grant	T16S, R31E, sec. 6	1450	Private	45	1.2	17.8
15**	Grant	T16S, R31E, sec. 28	1430	Private	10	1.2	8.8

*Localities obtained from Bureau of Land Management 30-min series maps

**No evidence of occupancy by pygmy rabbits detected in 1983 tats and one livestock exclosure. However, mean shrub cover in areas occupied by pygmy rabbits in Oregon (28.8 ± 1.4%) was much less than the 46% in Idaho, and mean shrub height in Oregon (84.4 ± 5.8 cm) was significantly greater than the 56 ± 2.8 cm in Idaho (Green and Flinders 1980b). We suspect that observed differences in shrub cover, in part, were the result of different methods used to make the estimates. The significant difference in shrub height possibly resulted from our decision to delimit occupied areas to within 100 m of peripheral burrows, because mean shrub height at occupied and adjacent sites combined was 65.5 ± 5.0 cm, not significantly different from that reported in Idaho (Green and Flinders 1980b).

There was relatively little overlap for sites occupied by pygmy rabbits and adjacent sites based on measurements of vegetative and soil characteristics (Fig. 2). Correlations between 10 habitat variables used in discriminant analysis and the discriminant function showed that shrub cover best distinguished sites occupied by pygmy rabbits from adjacent sites ($r = 0.71$), followed by soil depth ($r = 0.48$), mean shrub height ($r = 0.46$), soil strength at surface ($r = 0.27$), and subsurface horizons ($r = 0.19$). Percent basal area of perennial grasses, density of annual grasses, density of forbs, and components of soil texture contributed little to the separation of occupied and adjacent habitats ($|r| < 0.13$). Pearson correlation coefficients calculated for habitat variables measured at sites occupied by *S. idahoensis* and adjacent sites showed soil depth was correlated positively with shrub cover ($r = 0.64$) and shrub height ($r = 0.71$) and negatively with soil strengths of surface ($r = -0.48$) and subsurface ($r = -0.57$) horizons.

The mean number of entrances per burrow at each of the 15 occupied sites sampled was the dependent variable used in stepwise-multiple regression; soil depth, percent slope, strengths of surface and subsurface soils, and percent sand and percent silt at surface and subsurface soil horizons were dependent variables (Tables 1 and 2). The best model (Neter and Wasserman 1974) showed number of burrow entrances varied inversely with slope and subsurface soil strength ($R^2 = 0.55$).

Of 427 samples analyzed to identify subspecies of *Artemisia tridentata*, 120 were *A. t. vaseyana*, 101 were *A. t. tridentata*, and 167 were *A. t. wyomingensis*; 84 could not be

Table 2. Means, standard errors of means, and ranges of habitat variables measured at 13 sites occupied by pygmy rabbits and 21 sites adjacent thereto, Oregon, 1982.

Habitat variable	Occupied sites $\bar{X} \pm$ S.E.	Occupied sites Range	Unoccupied sites* $\bar{X} \pm$ S.E.	Unoccupied sites* Range
Shrub cover (%)**	28.8 ± 1.4	21.0–36.2	17.7 ± 1.2	13.9–27.1
Artemisia spp. cover (%)**	23.7 ± 1.4	16.3–33.2	14.8 ± 1.5	3.3–26.6
Shrub height (cm)**	84.4 ± 5.8	55.8–115.2	52.7 ± 5.3	24.2–86.9
Artemisia spp. height (cm)**	90.8 ± 5.8	67.7–126.6	56.9 ± 6.1	26.2–103.7
Perennial grasses percent basal area	3.7 ± 0.9	0.0–9.8	4.2 ± 0.7	0.0–9.4
Annual grasses density (n/1,000 cm^2)	5.2 ± 2.1	0.0–20.6	5.6 ± 3.6	0.0–46.2
Forb density (n/1,000 cm^2)	3.4 ± 0.6	0.2–6.3	4.3 ± 1.0	0.2–11.4
Cryptogam cover (%)	2.4 ± 0.5	0.1–5.4	2.3 ± 0.4	0.0–4.5
Soil depth (cm)**	51.0 ± 2.3	36.2–60.0	31.0 ± 3.1	16.3–52.6
Soil strength (kg/cm^2)				
Surface **	0.8 ± 0.2	0.2–2.4	1.9 ± 0.4	0.3–4.7
Subsurface (40 cm)**	3.8 ± 0.3	1.2–5.0	4.6 ± 0.2	2.0–5.0
Soil texture (surface)				
Sand (%)	51.1 ± 2.7	35.7–71.1	48.8 ± 3.2	25.5–65.8
Silt (%)	30.4 ± 2.1	16.6–44.7	31.8 ± 2.3	20.7–45.3
Clay (%)	18.5 ± 1.5	10.5–26.1	19.9 ± 2.2	13.0–41.2
Soil texture (subsurface)				
Sand (%)	50.2 ± 3.9	32.5–81.2	43.0 ± 4.6	24.8–68.8
Silt (%)	27.0 ± 2.1	12.0–35.8	26.4 ± 2.3	16.6–44.1
Clay (%)**	22.8 ± 2.7	6.8–36.9	30.5 ± 3.5	10.8–48.2

*Represents average where more than one area was sampled adjacent to occupied site

**Two-tailed paired t test indicated means of differences of occupied and adjacent sites were significantly different ($P < 0.05$) from zero

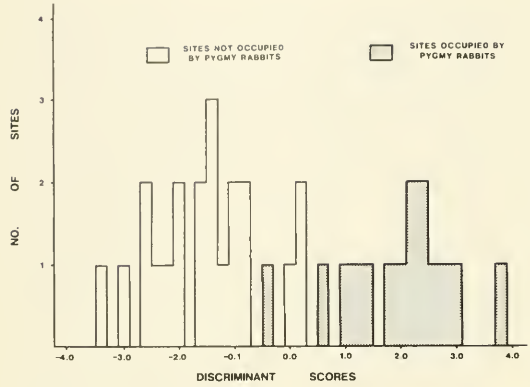

Fig. 2. Frequency histogram of discriminant scores of 15 sites occupied by pygmy rabbits (centroid = 1.96), and 21 adjacent sites not occupied by pygmy rabbits (centroid = -1.47), Oregon, 1982.

identified by criteria of Shumar et al. (1982). Shrubs associated with four sites occupied by S. *idahoensis* were pure stands of *A. t. vaseyana* (Table 3). At remaining sites, stands were mixtures of *A. t. tridentata*, *A. t. wyomingensis*, and unidentified subspecies (possibly hybrids). Two sites had high densities of *A. t. tridentata* and at two sites *A. t. wyomingensis* was predominant (Table 3).

No evidence of recent activity of pygmy rabbits was evident at 10 of 15 sites occupied in 1982 when reexamined in April and July 1983 (Table 1). Of 51 burrows at five sites occupied in 1982, 19 were open in July 1983, and only 8 had relatively fresh fecal pellets of pygmy rabbits in the vicinity.

Discussion and Conclusions

This study, the first attempt to quantify both soil and vegetative characteristics at sites occupied by pygmy rabbits, demonstrated that S. *idahoensis* in Oregon inhabited areas where soils were significantly deeper and looser than at adjacent sites. Soil depth and soil strength, more than soil texture, were physical properties of soil that distinguished sites occupied by pygmy rabbits from adjacent sites, and probably were related to excavation of burrows. Mean soil depth at 13 sites occupied by pygmy rabbits in Oregon (Table 2) approximated depths of burrows reported elsewhere (Grinnell et al. 1930, Bailey 1936, Bradfield 1975), supporting the belief that pygmy rabbits burrowed only where soil depth was sufficient (Wilde 1978). In Oregon, the inverse relationship between number of burrow entrances and soil strength indicated that softer soils facilitated burrow construction. However, the significant inverse relationship between number of burrow entrances and percent slope cannot be explained on the basis of the present knowledge of the biology of the species.

Initially we hypothetized that distribution of pygmy rabbits was determined, in part, by relative abundances of various subspecies of *Artemisia tridentata*. The shrub constituted a major portion of the diet of S. *idahoensis* in Idaho (Wilde 1978, Green and Flinders 1980b), and preliminary observations by Green and Flinders (1980b) indicated that specific subspecies were consumed. Our findings did not support the hypothesis; additional evidence that the distribution of S. *idahoensis* was not linked to specific subspecies of *A. tridentata* was provided by feeding trials of captives in which consumption of *A. t. tridentata* and *A. t. vaseyana* was not significantly different (White et al. 1982).

Although abundance of grasses and forbs were not primary factors that distinguished sites occupied by pygmy rabbits from adjacent sites in Oregon (Table 2) or in Idaho (Green and Flinders 1980b), areas with dense stands of cheatgrass (*Bromus tectorum*) seemingly were avoided because only 2 of 51 sites occupied by S. *idahoensis* in Oregon contained appreciable stands; both were adjacent to asphalt highways. In areas where cheatgrass and other annual grasses were dense, our ability to observe rabbits, burrows, and fecal pellets possibly was reduced. Green and Flinders (1980b) reported that mean biomass of forbs was significantly greater and that of grasses significantly less at sites where S. *idahoensis* was most abundant, and concluded that differential consumption of grasses and forbs by the species was responsible. In Oregon, low density of cheatgrass at sites occupied by pygmy rabbits was not the result of foraging by rabbits; densities of annual grasses were not significantly different between occupied and adjacent sites. We suspect that annual grasses restricted movements or vision of pygmy rabbits and were avoided to improve chances of escaping from predators (Yahner 1982).

The affinity exhibited by pygmy rabbits for areas with greater shrub cover and height possibly also was related to predator avoidance because, compared with larger leporids, pygmy rabbits are relatively slow and vulnerable in open habitats (Bailey 1936, Orr 1940). However, they are better able to elude pursuers amidst shrubs (Anthony 1913, Bailey 1936, Orr 1940, Severaid 1950, Wilde 1978). In addition, greater shrub cover represents additional food resources because pygmy rabbits forage extensively on sagebrush, even climbing the shrubs to do so (Janson 1946). Similar conclusions regarding association with shrubs for avoidance of predators and for increasing the resource base were provided for other small desert mammals (Rosenzweig et al. 1975, Beatley 1976, Hallett 1982, Thompson 1982). Shrub cover may be especially critical in winter for a species poorly adapted for climbing when 99% of the diet of S. *idahoensis* is sagebrush (Green and Flinders 1980a) and snow accumulations may cover other food resources but permit easy access to distal parts of shrubs (Bradfield 1975).

A marked decline in evidence of pygmy rabbits at sample sites in 1983 demonstrated that populations were susceptible to rapid declines and possibly local extirpation. Other researchers detected similar declines in populations of pygmy rabbits (Janson 1946, Bradfield 1975, J. T. Flinders, pers. comm.), but Wilde (1978), after a 2.5-year study of a population in Idaho, concluded that S. *idahoensis* was a "high inertia" species with reduced capacity for rapid increase in density. The term *high inertia* was used by Murdoch (1970) to describe *K*-selected species; although not explicitly stated by Wilde (1978), the tendency for density of pygmy rabbit populations to be relatively stable could be inferred from his report. Our observations did not support such an inference, nor was it supported entirely by those of Wilde (1978), who abandoned one of three study sites when number of active burrows and trapping success declined.

Analysis of vegetation and soil characteristics at areas associated with pygmy rabbits in Oregon substantiated previous observations that this species inhabited islands of

Table 3. Subspecific identity of 472 samples of *Artemisia tridentata* collected at sites occupied by pygmy rabbits and adjacent sites not occupied by pygmy rabbits, Oregon, 1982.

	Occupied sites				Unoccupied sites			
Site number	*A. t. tridentata*	*A. t. wyomingensis*	*A. t. vaseyana*	Unknown	*A. t. tridentata*	*A. t. wyomingensis*	*A. t. vaseyana*	Unknown
1	15				10	5		
2	10	4		1	1	11		3
3°	6	9			11			4
					1	(14)		
4°	7	5		3	5	7		3
					(4)	(3)		(3)
5	4	9		2		14		1
6			15				15	
7°		13		2		14		1
						(12)		(3)
8	11	1		3				
9		4		11				
10°		4		11				14
						(5)		(8)
11		13		2		14		1
12°	3	6		6				
	(13)			(2)				
13			15				15	
14			15				15	
15			15				15	
Totals	69	68	60	43	32	99	60	41

°Values in parentheses obtained from repeated sampling at site habitat (Dice 1926, Davis 1939, Orr 1940) where dense or clumped stands of sagebrush (Anthony 1913, Grinnell et al. 1930, Bailey 1936, Severaid 1950, Bradfield 1975) grew in deep (Davis 1939, Campbell et al. 1982), loose (Orr 1940, Janson 1946) soils. Because of the specific nature of requisite soil and vegetative conditions, and because populations seem subject to perturbation and even local extirpation, successful dispersal of individuals from less affected populations into favorable habitats becomes crucial if pygmy rabbits are to persist as a component of the fauna of Oregon. Although their dispersal abilities are not understood clearly, pygmy rabbits are suspected of being reluctant or unable to cross open areas such as roads or lands cleared of sagebrush (Bradfield 1975, J. T. Flinders, pers. comm.); thus, dense stands of *A. tridentata* along streams, roads, and fencerows become avenues of dispersal (Green and Flinders 1980b). Concerns for pygmy rabbit populations traditionally have focused on habitat destruction associated with range and agricultural improvements (Green and Flinders 1980b, Holechek 1981). Fragmentation of sagebrush communities poses an additional threat to populations of pygmy rabbits by reducing the size of these communities and increasing their interstitial distances, but the severity of this threat cannot be assessed without better understanding the dispersal abilities of the species.

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Literature Cited

Anthony, H. E. 1913. Mammals of northern Malheur County, Oregon. Bull. Amer. Mus. Nat. Hist. 32:1–27.

Bailey, V. 1936. The mammals and life zones of Oregon. N. Amer. Fauna 55:1–416.

Beatley, J. C. 1976. Environments of kangaroo rats (*Dipodomys*) and effects of environmental change on populations in southern Nevada. J. Mammal. 57:67–93.

Bouyoucos, G. J. 1962. Hydrometer method improved for making particle size analysis of soils. Agron. J. 54:464–465.

Bradfield, T. 1975. On the behavior and ecology of the pygmy rabbit *Sylvilagus idahoensis*. Unpublished thesis. Idaho State Univ., Pocatello. 43 pp.

Campbell, T. M., III, T. W. Clark, and C. R. Groves. 1982. First record of pygmy rabbits (*Brachylagus idahoensis*) in Wyoming. Great Basin Nat. 39:88.

Daubenmier, R. F. 1959. A canopy coverage method of vegetational analysis. Northwest Sci. 33:43–64.

Davis, W. B. 1939. The recent mammals of Idaho. Caxton Printers Ltd., Caldwell, Idaho. 400 pp.

Dice, L. R. 1926. Notes on the Pacific Coast rabbits and pikas. Occas. Papers, Mus. Zool. Univ. Michigan. 166:1–28.

Green, J. S., and J. T. Flinders. 1980a. Brachylagus idahoensis. Mammal. Species 125:1–4.

______. 1980b. Habitat and dietary relationships of the pygmy rabbit. J. Range Manage. 33:136–142.

Grinnell, J., J. Dixon, and J. M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. California Publ. Zool. 35:1–594.

Hall, E. R. 1981. The mammals of North America. 2d ed., John Wiley and Sons, New York. 1:xv + 1–600 + 90.

Hallett, J. G. 1982. Habitat selection and the community matrix of a desert small-mammal fauna. Ecology 63:1400–1410.

Holechek, J. L. 1981. Brush control impacts on rangeland wildlife. J. Soil Water Conserv. 36:265–269.

Janson, R. G. 1946. A survey of the native rabbits of Utah with reference to their life histories and ecology. Unpublished thesis. Utah State Agric. Coll., Logan. 103 pp.

Klecka, W. R. 1975. Discriminant analysis. Pages 434–462 *in* W. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds., Statistical package for the social sciences. 2d ed., McGraw-Hill, New York. 675 pp.

Murdoch, W. W. 1970. Population regulation and population inertia. Ecology 51:497–503.

Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois. 842 pp.

Olterman, J. H., and B. J. Verts. 1972. Endangered plants and animals of Oregon. *IV Mammals*. Oregon Agric. Expt. Sta., Spec. Rept. 364:1–47.

Oregon Water Resource Board. 1969. Oregon's long range requirements for water. Oregon Agric. Expt. Sta. and U.S. Dept. Agric. Soil Conserv. Serv., Appendix I-5:1–116; I-6:1–101; I-7:1–73; I-10:1–85; I-11:1–72; I-12:1–79; I-14:1–77.

ORR, R. T. 1940. The rabbits of California. Occas. Papers California Acad. Sci. 19:1–227.

PIEPER, R. D. 1978. Measurement techniques for herbaceous and shrubby vegetation. New Mexico State Univ. Press, Las Cruces. 148 pp.

ROSENZWEIG, M. L., B. SMIGEL, AND A. KRAFT. 1975. Patterns of food, space, and diversity. Pages 241–268 *in* I. Prakash and P. K. Ghosh, eds., Rodents in desert environments. W. Junk, The Hague. 624 pp.

SEVERAID, J. H. 1950. The pygmy rabbit (*Sylvilagus idahoensis*) in Mono County, California. J. Mammal. 31:1–4.

SHUMAR, M. L., J. E. ANDERSON, AND T. D. REYNOLDS. 1982. Identification of subspecies of big sagebrush by ultraviolet spectrophotometry. J. Range Manage. 35:60–62.

THOMPSON, S. D. 1982. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. Ecology 63:1303–1312.

WHITE, S. M., J. T. FLINDERS, AND B. L. WELCH. 1982. Preference of pygmy rabbits (*Brachylagus idahoensis*) for various populations of big sagebrush (*Artemisia tridentata*). J. Range Manage. 35:724–726.

WILDE, D. B. 1978. A population analysis of the pygmy rabbit (*Sylvilagus idahoensis*) on the INEL site. Unpublished dissertation, Idaho State Univ., Pocatello. 172 pp.

WILDE, D. B., J. S. FISHER, AND B. L. KELLER. 1976. A demographic analysis of the pygmy rabbit *Sylvilagus idahoensis*. Pages 88–105 *in* O. D. Markham, ed., 1975 Progress report Idaho National Engineering Laboratory Site radioecology-ecology programs. U.S. Energy Res. and Devel. Admin., Idaho Falls. 205 pp.

WINWARD, A. H., AND E. W. TISDALE. 1969. A simplified chemical method for sagebrush identification. Univ. Idaho Forest, Wildl. and Range Expt. Sta. Bull. 11:1–2.

YAHNER, R. H. 1982. Microhabitat use by small mammals in farmstead shelterbelts. J. Mammal. 63:440–445.

LATE SUMMER CHANGES IN MULE DEER DIETS WITH INCREASING USE ON BITTERBRUSH RANGELAND[1]

D. D. Austin[2], P. J. Urness[2], and J. King[3]

Abstract.— Late summer diet composition of mule deer was determined daily within a mountain browse enclosure dominated by antelope bitterbrush. Palatable forages of low abundance were rapidly depleted, and bitterbrush continually composed over 50% of the diet, even at utilization exceeding 350 deer-days/ha. The relationship of bitterbrush forage production and deer-days use is discussed.

Documentation clearly shows that rangelands containing antelope bitterbrush (*Purshia tridentata*) are important to mule deer (*Odocoileus hemionus*) in winter (Kufeld et al. 1973). Furthermore, on low elevation ranges where succulent forages are scarce, bitterbrush has been reported a major and palatable contribution to summer diets (Leach 1956, Lesperance et al. 1970, Trout and Thiessen 1973, Tueller and Monroe 1976, Tueller 1979, Austin and Urness 1983). Although these summer studies have shown the importance of bitterbrush, they have provided only limited information on changes in diet as preferred forages are depleted. This paper reports progressive dietary changes in a short-duration, high-intensity grazing trial (totaling 356 deer-days/ha; 144 dd/ac) and develops a guideline for estimating potential summer deer-days use on comparable rangeland sites.

Methods

An enclosure containing .07 ha (.17 ac) was constructed on the West Tintic Mountains at 1970 m (6460 ft) elevation in Tooele County, Utah. Three tame, adult female mule deer were used to determine diets. Although studies concerned primarily with comparing wild and tame deer are unavailable, the assumption that tame deer are behaviorally comparable to wild deer is supported by secondary findings of several researchers (Healy 1971, Willms and McLean 1978, Holl et al. 1979, Bartmann 1982, Austin et al. 1983). Deer were allowed to graze freely within the enclosure, and forage selection (bites by species) was recorded each morning and evening for about three hours during a consecutive eight-day trial in late August 1982. During grazing periods each deer was observed alternately for 20 minutes. Data were initially summarized by individual days. Because of diet similarities between some days and evident differences between others, however, the data were collapsed into four unequal periods. Diets were determined as percent dry weight consumption by species using hand-plucked simulated bites (Deschamp et al. 1979).

Vegetal production, and forage availability after grazing, within the enclosure were determined by sampling immediately before and after the grazing trial from 25 evenly spaced 1 m^2 (10 ft^2) circular plots established on a predetermined grid. Half of each plot was clipped before (south half) and after (north half) grazing. Forage utilization of plant species by deer was determined as the difference between pre- and postgrazing clippings. Weight by species was measured to the nearest gram and converted to dry weight from oven-dried samples.

Palatable plant species were defined as having the initial ratio of percent diet contribution divided by percent vegetal production greater than 1.0, and the ratio for unpalatable species was less than 1.0 (Neff 1974). Because palatability for individual species varies with season and vegetal community, palatabilities indicated below cannot be applied to other areas of differing habitat (Welch et al. 1981).

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Results

Vegetal production within the enclosure (Table 1) was dominated by browse (61%), with the remainder a mixture of grasses (19%), primarily bluebunch wheatgrass (*Agropyron spicatum*), forbs (11%), and cacti (9%). Total production was almost 900 kg/ha (800 lbs/ac). Bitterbrush composed 31% of the total browse, and unpalatable browse species contributed 67%.

During the 8-day trial, with each day equal to a grazing pressure of about 45 deer-days/ha (18 dd/ac), a total of 22,865 bites was recorded. The first period, 0–45 deer-days/ha (0–18 dd/ac), showed high dietary contribution of palatable species of low abundance, including Utah serviceberry (*Amelanchier utahensis*), mountain snowberry (*Symphoricarpos oreophilus*), common bastard toadflax (*Commandra umbellata*), and wayside gromwell (*Lithospermum ruderale*). These species composed 36% of the diet in the first period, but contributed less than 4% for subsequent periods (Table 1).

During period 2, 46–178 deer-days/ha (19–72 dd/ac), bitterbrush composed most of the diet as other palatable species became increasingly scarce (Table 1). Although unpalatable browse and grass were mostly ignored, most forbs were taken when found.

Period 3, 179–267 deer-days/ha (73–108 dd/ac), showed a slow shift toward the use of unpalatable forages as bitterbrush forage became less abundant and its proportion in the diet declined. This trend continued through period 4, with unpalatable browse and grass increasing in dietary contribution.

At the end of the trial, utilization of palatable shrubs exceeded 90%, and use of both cured and green forbs averaged about 80%. Use of unpalatable shrubs was much lower, with no use of pricklypear (*Opuntia* spp.). The figure of 48% utilization for mountain big sagebrush (*Artemisia tridentata vaseyana*) was probably somewhat inflated, as evidenced by its low dietary contribution (Table 1), and probably resulted from sampling insufficient plots for its uneven spacing. Since grass use (29%) included the effects of trampling, the actual percentage of forage used would likely be considerably less (Austin et al. 1983).

Discussion

It is evident from our data that considerable deer-days use can be supplied in sum-

Table 1. Vegetal production (kg/ha), deer diet composition (%) within grazing periods (± standard error), and forage utilization (%) in a bitterbrush rangeland exclosure.

Vegetal class	Species	Production	Grazing periods (deer-days/ha)				Forage utilization
			0–45	46–178	179–267	268–356	
Palatable shrubs	*Purshia tridentata*	172.3	51.8 ± 16.9	82.3 ± 1.4	74.7 ± 6.8	69.1 ± 9.9	93
	Amelanchier utahensis	5.6	9.3 ± 9.2	0.8	0.3	1.2 ± 1.2	93
	Symphoricarpos oreophilus	3.9	8.2 ± 4.9	0.6	0.3	0.3	90
Unpalatable shrubs	*Chrysothamnus viscidiflorus*	96.3	0.0	0.2	5.6 ± 3.9	10.9 ± 7.0	44
	Artemisia tridentata	69.8	0.0	0.2	3.2 ± 0.4	1.8 ± 1.8	48
	Juniperus osteosperma	200.4	0.7	2.2 ± 1.4	1.0 ± 0.6	2.5 ± 2.7	7
Cured forbs	*Crepis accuminata*	20.1	4.6 ± 1.5	2.1 ± 1.0	2.5 ± 0.7	2.4 ± 0.8	82
	Lupinus caudatus	3.0	0.6	3.3 ± 1.8	1.8 ± 1.3	2.0 ± 1.6	75
	Balsamorhiza hispida	8.6	0.5	0.7	2.4 ± 1.5	1.5 ± 1.1	74
	9 others	27.6	3.4 ± 1.5	3.4 ± 2.3	2.1 ± 0.7	1.9 ± 0.8	62
Green forbs	*Commandra umbellata*	18.9	9.9 ± 5.9	3.0 ± 1.6	1.7 ± 0.9	0.9	85
	Lithospermum ruderale	13.6	8.9 ± 9.4	0.4	0.0	0.0	85
	5 others	11.4	2.0 ± 2.1	0.5	0.4	0.1	93
Cacti	*Opuntia* spp.	76.8	0.0	0.0	0.0	0.0	0
Grasses	Gramineae	169.0	0.1	0.3	4.0 ± 2.9	5.4 ± 3.5	29
Total		897.3					

mer by bitterbrush rangelands. In addition to the deer use, grazing by livestock to utilize the grass resource and maintain the bitterbrush stand should be applied in spring when grass is succulent (Smith and Doell 1968, Jensen et al. 1972, Austin and Urness 1983).

Since bitterbrush comprises a high proportion of the summer diet where other palatable forages are scarce, a direct relationship between potential deer use and bitterbrush production seems reasonable. Austin and Urness (1983) reported that 122 deer-days/ha (49 dd/ac) use was reasonable for a similar area where bitterbrush production was 130 kg/ha (116 lbs/ac). In their analyses it was assumed that daily dry weight intake of bitterbrush averaged 1.5 kg/deer-day and utilization of current annual growth was 70%. In this study, 172 kg/ha (153 lbs..c) of bitterbrush forage was available and 178 deer-days/ha (72 dd/ac) use accrued before diets began changing due to depletion of bitterbrush. From these data, we suggest that dry weight production (kg/ha) of bitterbrush be numerically equated to summer deer-days/ha use as a first approximation. In our study area where winter use by deer is small, reserving bitterbrush forage is unnecessary; however, adjustments may be needed on areas where winter use is significant.

Literature Cited

Austin, D. D., and P. J. Urness. 1983. Summer use of bitterbrush rangeland by mule deer. Pages 203–212 *in* A. Tiedemann and K. Johnson, eds., Bitterbrush and Cliffrose Symposium.

Austin, D. D., P. J. Urness, and L. C. Fierro. 1983. Spring livestock grazing affects crested wheatgrass regrowth and winter use by mule deer. J. Range Manage. 36:589–593.

Bartmann, R. M. 1982. Evaluation of winter food choices by tame mule deer. J. Wildl. Manage. 46:807–812.

Deschamp, J. A., P. J. Urness, and D. D. Austin. 1979. Summer diets of mule deer from lodgepole pine habitats. J. Wildl. Manage. 43:154–161.

Healy, W. M. 1971. Forage preferences of tame deer in a northwest Pennsylvania clear-cutting. J. Wildl. Manage. 35:717–723.

Holl, S. A., H. Salwasser, and B. Browning. 1979. The diet composition and energy reserves of California mule deer during pregnancy. California Fish and Game 65:68–79.

Kufeld, R. C., O. C. Wallmo, and C. Feddema. 1973. Foods of the Rocky Mountain mule deer. USDA Rocky Mtn. For. and Range Exp. Sta. Res. Pap. RM-111. 31 pp.

Jensen, C. H., A. D. Smith, and G. W. Scotter. 1972. Guidelines for grazing sheep on rangelands used by big game in winter. J. Range Manage. 25:346–352.

Leach, H. K. 1956. Food habits of the great basin deer herds of California. California Fish and Game 42:243–308.

Lesperance, A. L., P. T. Tueller, and V. R. Bohman. 1970. Symposium on pasture methods for maximum production in beef cattle: competitive use of the range resource. J. Anim. Sci. 30:115–121.

Neff, D. J. 1974. Forage preferences of trained mule deer on Beaver Creek watersheds. Ariz. Game and Fish Dept. Spec. Rep. 4. 61 pp.

Smith, A. D., and D. D. Doell. 1968. Guidelines to allocating forage between cattle and big game on winter ranges. Utah Div. Wildl. Res. Publ. No. 18-11. 32 pp.

Trout, L. E., and J. L. Thiessen. 1973. Physical condition and range relationships of the Owyhee deer herd. Job completion Rep. Proj. W-141-R-2. Idaho Fish and Game Dept. 37 pp.

Tueller, P. T. 1979. Food habits and nutrition on Nevada ranges. Nevada Agric. Expt. Sta. Publ. 128, Univ. of Nevada, Reno. 124 pp.

Tueller, P. T., and L. A. Monroe. 1976. Management guidelines for selected deer habitats in Nevada. Nevada Agric. Expt. Sta. Publ. R104, Univ. of Nevada, Reno. 85 pp.

Welch, B. L., E. D. McArthur, and J. N. Davis. 1981. Differential preference of wintering mule deer for accessions of big sagebrush and for black sagebrush. J. Range Manage. 34:409–411.

Willms, W., and A. McLean. 1978. Spring forage selection by tame mule deer on big sagebrush range, British Columbia. J. Range Manage. 31:192–199.

INSECT DAMAGE, CONE DIMENSIONS, AND SEED PRODUCTION IN CROWN LEVELS OF PONDEROSA PINE

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Abstract.— Insect damage to second-year cones was generally not significantly different between crown levels, but was significantly different among areas and among trees within areas for *Conophthorus*, *Megastigmus*, and *Cydia*. Both cone length and width were not significantly different between lower and middle crown, but cone length was significantly greater in the upper crown. Seeds per cone ranged from 34 to 66, but the percent of sound seed per cone varied significantly according to the amount of insect damage.

Cone and seed insects of ponderosa pine, *Pinus ponderosa* Douglas ex Lawson, have received little attention in the Southwest. In southern New Mexico Kinzer et al. (1972) identified the most common insects associated with ponderosa pine cones and determined the extent of their damage. In California Koerber (1967) identified the insect complex affecting ponderosa pine seed production and assessed the incidence of damage by the more important species. Between these two locations, little work had been done until an initial survey by Ragenovich et al. (1981) confirmed the presence of the most common species found by Kinzer et al. (1972) and determined the extent of their damage. A more extensive study by Schmid in 1982 had to confine sampling to that portion of the lower crown within reach of a step ladder. The question naturally arose as to whether the incidence of insect damage was different among crown levels. The present study determined the incidence of insect damage in second-year cones from different crown levels within the same tree; it also determined the dimensions of cones and their seed production.

Methods

Maturing pine cones were collected from 10 locations on the Coconino and Kaibab National Forests (southern part) in northern Arizona during September 1982 (Fig. 1). Sixteen cones were randomly pruned from the lower and middle crowns of each of 10 co-dominant or dominant trees at each of 8 locations. At 2 locations, cone-bearing trees were either felled or climbed by Forest Service personnel, and cones were collected also from the upper crowns, which are normally unreachable with a pole pruner. The cones were sacked, labeled by tree number, crown level, and location, and placed in cold-storage units in Flagstaff.

To determine the percentage of seeds damaged by insects, each cone was dissected.

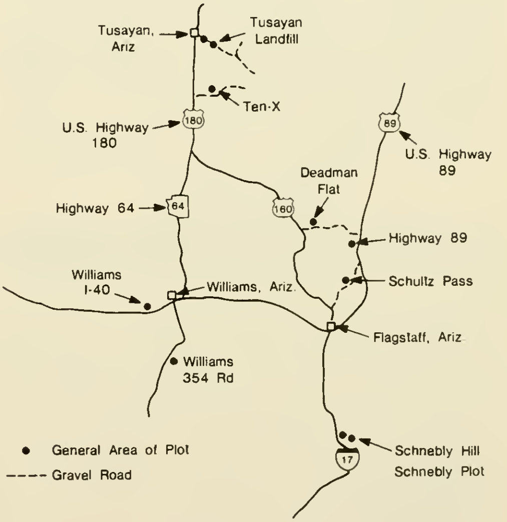

Fig. 1. Location of cone collection areas on the Coconino and Kaibab national forests.

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Cone length and width, and number of sound, hollow, and insect-damaged seeds were recorded. The percentage of seeds damaged by insect species was determined for each cone. Because *Conophthorus* and *Dioryctria* destroyed 100% of the seeds in each infested cone nearly all the time and *Megastigmus* and *Cydia* damaged variable percentages in each cone, the percentage of cones damaged by *Conophthorus* and *Dioryctria* and the percentage of seeds per cone damaged by *Megastigmus* and *Cydia* were each subjected to analysis of variance testing for significant variation among locations and trees and between crown levels ($\propto$ = 0.05). Prior to analysis, homogeneity of variance was evaluated for each set of data and, where nonhomogeneous variance occurred, the data were transformed using either an arcsine, square root, or square transformation and then the analysis was performed. Tukey's multiple range test was used to determine which mean values were significantly different from each other when the ANOV showed significant differences occurring. Confidence intervals (0.95) were computed for each mean using the Bonferroni method. Means and confidence intervals were then back-transformed to derive the information presented in the tables. Entries in Table 4 are based on untransformed data and variations among individual tree averages.

RESULTS AND DISCUSSION

Insect Damage

The amount of insect damage to cones and seeds was not significantly different between the lower crown and the middle or upper crown for either *Conophthorus ponderosae* Hopkins, *Dioryctria* spp., or *Cydia* sp. and was significantly greater in the upper levels for *Megastigmus albifrons* Walker in only one location. Percent of cones damaged by *Conophthorus* (Table 1) varied significantly among areas and among trees within areas, but did not vary significantly for *Dioryctria*. Similarly, the percentage of seeds per cone damaged by *Megastigmus* and *Cydia* (Table 2) varied significantly among areas and among trees within areas for both species.

The insignificant differences in insect damage between crown levels indicate that cones can be collected from any crown level to determine the incidence of damage for the tree. The significant differences in insect damage among areas and among trees within areas indicate other factors are influencing the degree of damage among trees and locations.

Conophthorus damage was substantial in three locations (Table 1). Although the mean values for all crown levels did not approach the 50% damage level cited by Pearson (1950) in the three locations, percent damage was 45% in the middle crown at the U.S. Highway 89 location. Because cone damage was greatest at the three highest locations and at the lowest location, elevation might be thought to be an important factor. However, other past and current cone studies have indicated an especially high incidence of *Conophthorus* damage at the Deadman Flat and U.S. Highway 89 locations, locations producing several consecutive cone crops. These observations suggest that locations producing cone crops each year may support a

TABLE 1. Mean percentage of cones infested by *Conophthorus* and *Dioryctria*, Coconino and Kaibab national forests, Arizona, 1982.

National forest/Location	Elevation	*Conophthorus*	*Dioryctria*
	m	$\bar{X}$(95% confidence interval)	
Coconino National Forest			
Schnebly Hill	1980	<1 (0–1)	0
Schnebly Plot	1980	<1 (0–1)	0
U.S. Highway 89	2195	39(12–66)	1(0–3)
Deadman Flat	2290	15 (6–24)	1(0–2)
Schultz Pass	2465	35(14–56)	1(0–3)
Kaibab National Forest			
U.S. Highway I-40	1800	31(13–50)	1(0–2)
Ten-X	2025	2 (0–5)	0
Tusayan	2045	1 (0–3)	0
Tusayan Landfill	2045	8 (0–16)	1(0–3)
Williams 354 Road	2165	0	0

TABLE 2. Mean percentage of seeds per cone infested by *Megastigmus* and *Cydia*, Coconino and Kaibab national forests, Arizona, 1982.

National forest/Location	Elevation	*Megastigmus*	*Cydia*
	m	$\bar{X}$(95% confidence interval)	
Coconino National Forest			
Schnebly Hill	1980	1 (1–2)	6 (0–10)
Schnebly Plot	1980	1 (<1–1)	0
U.S. Highway 89	2195	77(72–81)	16(10–20)
Deadman Flat	2290	31(28–35)	11 (7–13)
Schultz Pass	2465	22(19–26)	5 (0–8)
Kaibab National Forest			
U.S. Highway I-40	1800	3 (2–4)	9 (0–13)
Ten-X	2025	2 (1–3)	9 (5–11)
Tusayan	2045	2 (2–3)	4 (1–6)
Tusayan Landfill	2045	5 (4–6)[a]	3 (0–4)
Williams 354 Road	2165	3 (1–4)	14 (5–20)

[a] Upper crown levels had a significantly greater percent of infested seeds.

greater *Conophthorus* population and thereby sustain a greater incidence of damage. Beetle populations in such areas would spend less time searching for new cones and would sustain less dispersal mortality, so the probability of cone damage would be greater. In contrast, locations producing cone crops every 3–5 years would sustain lesser damage to each crop because adults of successive generations would have to search more extensively to find trees with cones and would therein be subject to greater mortality.

Megastigmus caused the greatest seed loss of any insect, including *Conophthorus*. Damage was greatest on the same Coconino National Forest locations as where significant *Conophthorus* damage occurred. The hypothesis regarding greater *Conophthorus* damage being associated with continuous cone production areas also appears pertinent to *Megastigmus*.

Cone Dimensions

Cone length varied significantly among areas and among trees within the same area, but cone width did not vary significantly among areas or trees (Table 3). Both cone length and width were not significantly different between the lower and middle crowns in all areas, but cones in the upper crowns were longer and wider than cones from the lower crowns in the two areas where cones were gathered from the upper crown. Within the range of elevations from which cones were collected, neither cone length nor width exhibited a trend with elevation, so cone dimensions appear to be influenced more by stand and site conditions than by elevation.

Seed Production

Total seeds per cone ranged from 34 to 66 (Table 4). Compared to the 31 seeds per cone

TABLE 3. Mean length and width of ponderosa pine cones, Coconino and Kaibab national forests, Arizona, 1982.

National forest/Location	Elevation	Length	Width
		$\bar{X}$ (95% confidence interval)	
Coconino National Forest	*m*	*cm*	*cm*
Schnebly Hill	1980	8.1(7.8–8.3)	3.4(3.3–3.4)
Schnebly Plot	1980	8.1(7.9–8.3)	3.2(3.1–3.3)
U.S. Highway 89	2195	6.2(6.0–6.4)	3.3(3.2–3.4)
Deadman Flat	2290	8.1(7.9–8.4)	4.0(3.8–4.1)
Schultz Pass	2465	7.0(6.8–7.2)	3.5(3.5–3.6)
Kaibab National Forest			
U.S. Highway I-40	1800	7.0(6.8–7.2)	3.6(3.5–3.6)
Ten-X	2025	8.9(8.7–9.1)	3.3(3.2–3.4)
Tusayan	2045	9.5(9.4–9.7)	3.6(3.5–3.7)
Tusayan Landfill	2045	7.7(7.6–7.9)	3.6(3.6–3.7)
Williams 354 Road	2165	7.7(7.5–8.0)	3.2(3.1–3.3)

TABLE 4. Mean percentage of sound, hollow, and insect-damaged seeds[a] and mean number of total seeds per cone by location, Coconino and Kaibab national forests, Arizona, 1982.

National forest/Location	Sound seeds	Hollow seeds	Insect-damaged seeds	Total seeds
		X̄ (95% confidence interval)		
Coconino National Forest	%	%	%	*No.*
Schnebly Hill	82(79–85)	15(12–18)	3 (1–4)	45(37–54)
Schnebly Plot	84(82–86)	15(13–16)	1 (0–2)	42(35–49)
U.S. Highway 89	2 (0–4)	8 (3–12)	91(85–97)	34(23–45)
Deadman Flat	38(29–46)	16(11–21)	46(35–57)	59(52–66)
Schultz Pass	41(27–55)	11 (6–16)	48(33–63)	57(48–66)
Kaibab National Forest				
U.S. Highway I-40	39(29–50)	29(20–38)	32(18–45)	48(39–57)
Ten-X	77(73–82)	16(14–19)	6 (2–10)	41(33–50)
Tusayan	83(79–86)	13(10–15)	5 (2–7)	53(47–60)
Tusayan Landfill	62(52–72)	27(17–36)	11 (3–20)	66(60–71)
Williams 354 Road	60(52–68)	33(25–42)	7 (2–12)	39(29–49)

[a] Mean percentages may not add to 100 because of rounding.

of Larson and Schubert (1970), the number of seeds per cone was 35% greater in all but one location.

Sound seed production varied significantly among areas (Table 4), and was noticeably less in areas with high incidences of *Conophthorus* and *Megastigmus* damage. The combined effect of all insects on the U.S. Highway 89 location essentially eliminated the production of viable seed for that location. Situations like this point out the need for a preliminary insect survey before an area is designated as a cone collection site. *Conophthorus* damage is easily seen at the time of cone collection; because a *Conophthorus*-infested cone usually produces no viable seed, the total seed production for each tree can be reduced by the percentage of infested cones on the tree. However, *Megastigimus* damage, and to a lesser extent *Dioryctria* and *Cydia* damage, can only be determined after the cones have been collected and dissected. If the *Megastigmus* damage approaches approximately 75% (e.g., Table 2, U.S. Highway 89 location), then probably less than 25% viable seed will be obtained from each cone. Thus, four times as many cones will have to be collected to produce the desired quantity of seed. Potential collection areas should be examined and a sample of cones assayed to determine insect damage before a major collection effort is initiated.

LITERATURE CITED

KINZER, H. G., B. J. RIDGILL, AND J. G. WATTS. 1972. Seed and cone insects of ponderosa pine. New Mexico State Univ. Agric. Expt. Bull. No. 594. 36 pp.

KOERBER, T. W. 1967. Studies of the insect complex affecting seed production of ponderosa pine in California. Unpublished dissertation. Univ. of California, Berkeley. 86 pp.

LARSON, M. M., AND G. H. SCHUBERT. 1970. Cone crops of ponderosa pine in central Arizona including the influence of Albert squirrels. USDA For. Serv. Res. Pap. RM-58. 15 pp. Rocky Mtn. For. and Range Expt. Sta., Fort Collins, Colorado.

PEARSON, G. A. 1950. Management of ponderosa pine in the Southwest. Monograph 6. U.S. Dept. of Agric. Washington, D.C. 218 pp.

RAGENOVICH, I. R., M. R. WAGNER, AND J. M. SCHMID. 1981. Insects associated with ponderosa pine cones. Kaibab National Forest, 1980. Unpublished report on file, Forest Pest Management, Southwestern Region, USDA Forest Service, Albuquerque, New Mexico. 7 pp.

ENVIRONMENTAL SITE CHARACTERISTICS AND INCIDENCE OF CHOKECHERRY BLACK KNOT IN UTAH

Sarah Ann Stewart[1] and D. J. Weber[1]

Abstract.— Black knot disease of chokecherries, induced by *Dibotryon morbosum* (Schw.) Th. & Syd., is widely distributed in Utah. The incidence of black knot was measured by determining the ratio of total black knot gall length to total stem length of plants and then expressing that value as a percentage of diseased stems in the sample plot. The environmental site factors measured were elevation, exposure, slope, soil pH, soil depth, distance to surface water, plant moisture stress, and associated vegetation. Numerical values were determined for each of these variables at each of 18 randomly located plots. Correlation coefficients for plant moisture stress and soil temperature were –.439 ($p = .065$) and –.440 ($p = .055$). Multiple regression analyses using plant moisture stress and soil temperature gave a regression coefficient of –.641 ($p = .05$). As plant moisture stress and soil temperature decreased, incidence of black knot increased.

Black knot, induced by *Dibotryon morbosum* (Schw.) Th. & Syd., is common on chokecherry (*Prunus virginiana*) in its native habitat throughout Utah. The disease is characterized by elongated black swellings on the stems and branches (Fig. 1). A slight swelling of the current season twigs in the fall is the first symptom of infection. The following spring, knots become larger, bark ruptures, and the surface of the gall becomes covered

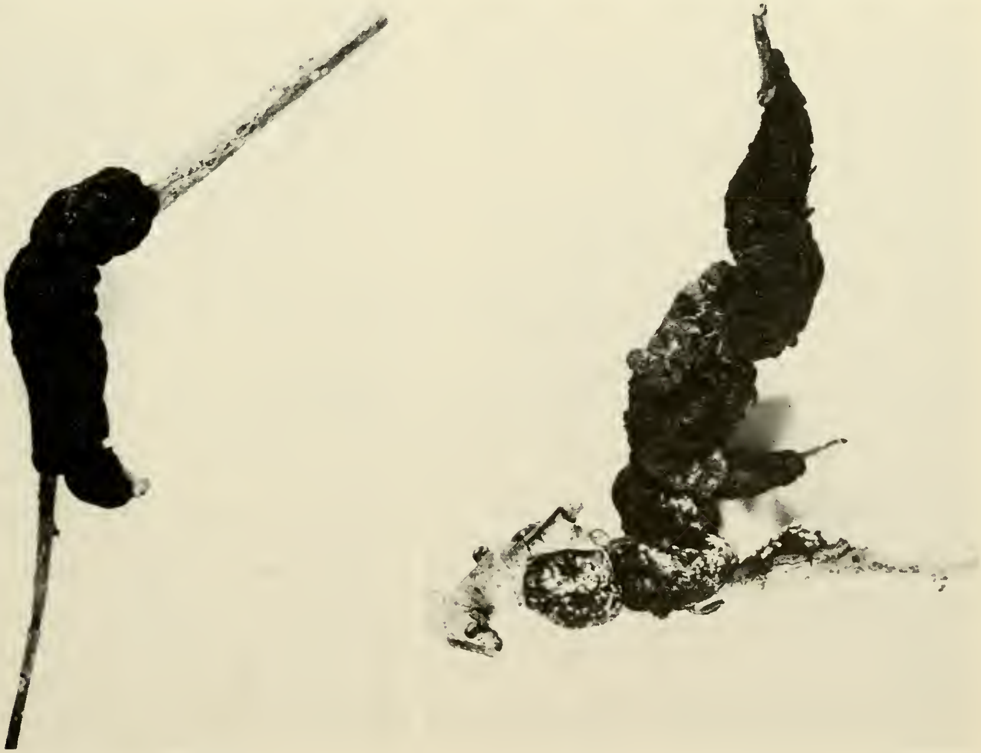

Fig. 1. Black knot on chokecherry.

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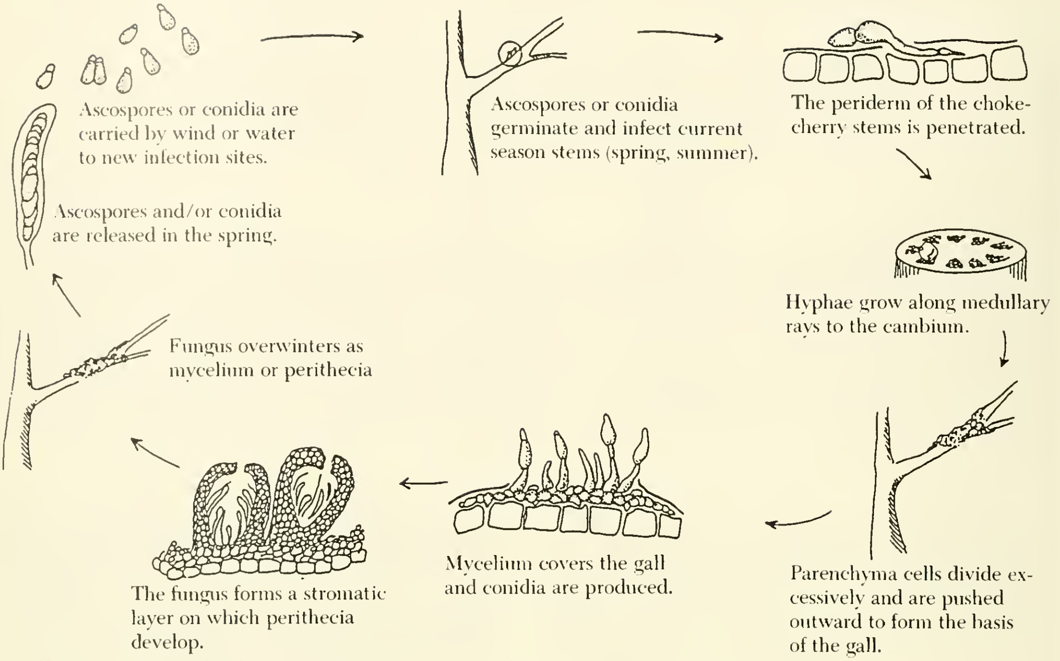
Ascospores or conidia are carried by wind or water to new infection sites.
Ascospores or conidia germinate and infect current season stems (spring, summer).
The periderm of the chokecherry stems is penetrated.
Hyphae grow along medullary rays to the cambium.
Parenchyma cells divide excessively and are pushed outward to form the basis of the gall.
Mycelium covers the gall and conidia are produced.
The fungus forms a stromatic layer on which perithecia develop.
Fungus overwinters as mycelium or perithecia
Ascospores and/or conidia are released in the spring.

Fig. 2. Disease cycle of *Dibotryon morbossum* on chokecherry (*Prunus virginiana*).

with a velvety green pad of mycelial tissue. By fall, the green surface is replaced by black stromatic tissue (Koch 1935a). The disease cycle is illustrated in Figure 2.

Dibotryon morbosum is an ascomycetous fungus. The light green ascospores are two celled, with one cell much smaller than the other. The light brown conidia that are produced early in the spring arise from greenish gall elevations formed the previous year (Anderson 1956). The perithecia are produced on the surface of the black knots in hemispherical, closely appressed elevations. Ascospores or conidia initiate the primary infection in the spring. Conidia germinate and penetrate intercellularly up to seven cell layers of periderm to initiate a primary infection. Initial infection usually occurs on current season's growth before layers of periderm are well developed, though occasionally a primary infection may occur on older twigs (Koch 1935b).

After periderm penetration, hyphae grow inward to the cambium and along the meduallary rays of the xylem. Initially no host cells are killed. When the mycelia reach the cambium, they stimulate parenchyma cells to divide excessively. These cells push outward and form the basis of developing knots. Mycelia grow internally in either direction and give rise to galls some distance from the original infection. During the second summer, the size of the knots enlarge and the fungus develops a stromatic surface layer on the knot in which perithecia are formed. Ascospores are discharged from perithecia in spring and are spread by air currents or water (Anderson 1956, Koch 1933, 1934, 1935a,b).

Since Koch's study (1933, 1934, 1935) of the epidemiology of black knot disease on horticultural plants, very little research has been done on the disease. There is little information on environmental site factors that correlate with intensity and distribution of black knot on native hosts. Previous research has been confined to horticultural varieties of the genus *Prunus*. Although Koch studied temperature and moisture as affecting ascospore and conidia ejection and germination, he did not relate these to incidence and distribution of the disease (Koch 1934). This investigation was designed to test the hypothesis that environmental site factors such as location in relation to water, plant moisture stress, soil pH, slope, aspect, and elevation may be used to characterize sites of high black knot incidence.

METHODS AND PROCEDURES

Forty .01 hectare plots were selected by random means using a gridded topographical map. Examination showed only 18 of the sites supported chokecherry; thus all subsequent analyses were confined to those sites. Potential plots were restricted to the area between the mouth of Provo Canyon and Cascade Springs in the Wasatch Mountains of Utah County, Utah. Data on the following site factors were collected from each site during September 1982; (1) elevation, (2) steepness of slope, (3) slope aspect, (4) soil depth, (5) soil pH, (6) soil temperature, (7) plant moisture stress, (8) distance to surface water, (9) estimate of understory cover, (10) estimate of composition (i.e., proportions of total cover contributed by forbs, grasses, and woody plants), (11) soil parent material, and (12) average age of chokecherry plants.

A numerical value was determined for slope aspect using the procedure of Beers et al. (1966) for aspect transformation. Soil depth was measured by pushing a pointed rod into the soil as far as the rod would go. Two to four soil depth readings were taken at each site and averaged. To maintain consistency, the same individual determined soil depth at all sites. Soil pH was determined using a glass electrode pH meter and a saturated soil paste. Plant moisture stress was determined by placing a chokecherry leaf into a plant moisture press and applying pressure until free water was exuded from the petiole (K. Harper, Brigham Young University, pers. comm.). Sample leaves were similar in size and taken from similar positions on plants. Several readings were taken from each site and averaged. Both plant moisture stress and soil temperature data were collected within a period of five days, between the hours of

TABLE 1. Environmental site factors associated with black knot disease of chokecherry.

Site	Chokecherry stem diameter (cm)	Infection (% stem length)	Average stem height (m)	Average age (yrs)	Plant moisture stress (bars)	% Understory cover	Elevation (m)	Aspect[1]	Slope degrees	Distribution surface H_2O (km)	Soil pH	Soil temperature (°C)	Soil depth (m)	Parent material
1.	2086	1.0	1.8	7	6.55	80	2073	.29	20	.4	7.0	12	.23	Quartzite
2.	4090	1.3	1.1	9	6.89	80	2012	.29	45	.5	6.8	13	.11	Limestone
3.	1082	3.0	.6	6	10.69	80	2134	1.00	30	.8	7.2	12	.29	Quartzite
4.	2770	1.4	1.2	6	6.89	95	2444	.29	45	1.6	6.9	10	.20	Quartzite
5.	6646	4.3	6.1	5	7.58	95	2256	1.71	30	.8	6.8	11	.54	Quartzite
6.	4450	10.9	4.3	9	6.55	85	2195	.00	70	.8	7.0	8	.23	Sandstone
7.	1708	10.9	1.9	7	6.55	90	2316	1.00	60	.0	6.7	10	.36	Quartzite
8.	16213	3.8	5.1	8	7.58	90	2438	.29	30	.2	6.9	10	.40	Quartzite
9.	3856	3.8	2.1	5	6.55	90	2256	1.71	5	.0	6.9	12	.45	Quartzite
10.	3812	.0	3.4	5	12.41	90	1890	.29	70	.4	7.2	13	.10	Quartzite
11.	2513	13.4	1.5	5	6.21	55	2073	1.71	60	.0	6.7	10	.23	Quartzite
12.	6367	.4	3.7	11	15.17	70	1840	.29	45	.0	7.1	10	.20	Slate
13.	4671	.0	2.9	10	10.34	25	1585	1.71	30	.4	6.9	10	.08	Limestone
14.	2556	.0	.5	3	11.72	70	2463	2.00	35	1.6	6.9	11	.40	Quartzite
15.	1622	.0	1.2	5	14.48	95	2463	.29	15	1.6	6.5	8	.34	Quartzite
16.	2761	1.0	.9	10	12.41	70	2073	.29	45	.4	7.3	12	.17	Qrtz/Sand
17.	5025	.0	5.0	10	8.27	25	1524	2.00	75	.0	7.3	14	.25	Quartzite
18.	4983	.0	5.8	5	3.45	95	1646	.29	30	.2	7.3	13	.44	Quartzite
Mean	4289.5	3.1	2.7	7	8.91	77	2093	.85	41	.5	7.0	11	.28	
SD	3373.1	4.3	1.9	2.4	3.24	22	300	.74	20	.6	.2	2	.13	

[1] Transformed as suggested by Beers et al. (1966).

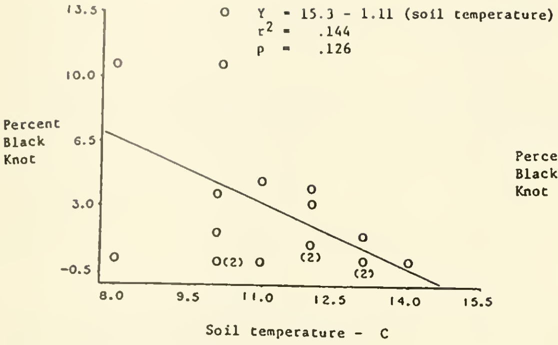

Fig. 3. Regression equation of percent black knot in relation to soil temperature.

0800 and 1000. To determine soil temperature, a soil temperature probe was inserted 15 cm into the soil. Average age of plants in a plot was determined by counting annual growth rings in stems of average diameter representative of the site.

All measurements on chokecherry plants and black knot galls were collected from four subplots (2 x 2 m) located in the corners of each of the 18 study plots. The degree of black knot infection was determined by measuring the length of all stems and branches of chokecherry and the length of black knot galls on the stems in each miniplot and expressing diseased tissue as a percentage of total stem length. Because of the rhizomatous, spreading growth habit of the chokecherry plant and difficulty of determining boundaries of a single plant, all stems and branches within the 2 x 2 m subplots were measured and considered as a single plant.

Correlation analyses, regression analyses, analysis of variance, and chi-square analysis were used to analyze the data. Regression and correlation coefficients were tested for significance with the t-test (Snedecor and Cochran 1967). To determine if elevation affected incidence of black knot, the plots were divided into three elevational categories with six plots in each category designated. Low elevation was 1524–2012 m. Midelevation was 2073–2256 m. High elevation was 2256–2463 m.

Results

Black knot disease was observed on plots between 1840 and 2444 m. The 18 random plots ranged in elevation from 1524 to 2463 m (5,000–8,000 ft) above sea level (Table 1). A chi-square analysis showed no significant difference in incidence of disease in high, middle, and low elevational categories.

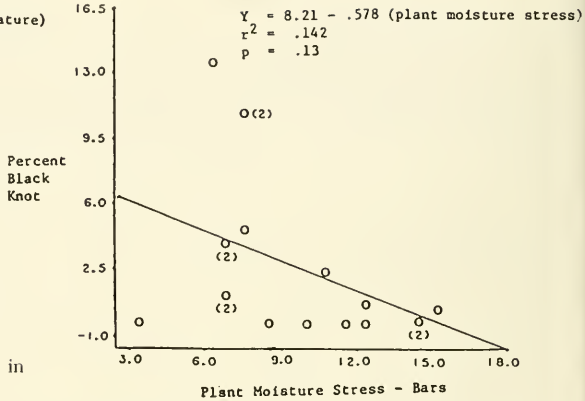

Fig. 4. Regression equation of percent black knot in relation to plant moisture stress.

The data obtained for the 12 factors on the 18 sites are shown in Table 1. A correlation analysis relating the incidence of black knot with all quantified site factors was determined. The correlation coefficients for the analyses are shown in Table 2. The correlation analyses indicate that black knot disease tended to occur more frequently on sites with lower soil temperatures, deeper soils, more acid soils, and lower plant moisture stress. Of these, soil temperature and plant moisture stress were most closely correlated with incidence of the disease. Both plant moisture stress and soil temperature were negatively correlated with disease incidence. The probability of the null hypothesis being true for plant moisture stress was .065; for soil temperature probability was .055.

Using severity of black knot as the dependent variable, linear regressions were determined with plant moisture stress or soil temperature as independent variables. Figures 3 and 4 show the results of those regression analyses. As plant moisture stress increased, severity of black knot decreased. Similarly, as soil temperature increased, incidence of black knot again decreased.

Since plant moisture stress and soil temperature were not significantly correlated with each other and could conceivably interact to alter plant response to black knot disease,

Table 2. Linear correlation coefficients showing relationship of degree of development of black knot disease (cm of gall/cm of stem) to various factors.

Factors	Correlation coefficient	Significance level (p)
Soil temperature	-.440	.055
Plant moisture stress	-.439	.065
Soil pH	-.391	.085
Distance to surface H_2O	-.264	N.S.
Average age of stand	-.086	N.S.
Average height of stems	-.002	N.S.
Slope	.353	.080
Elevation	.287	N.S.
% composition from forbs	.215	N.S.
Soil depth	.151	N.S.
Exposure	.110	N.S.
Percent understory cover	.101	N.S.
% composition from grasses	.061	N.S.
% composition from shrubs	.033	N.S.

N.S. = Nonsignificant

these two factors were used as independent variables in a multiple regression analysis in which degree of severity was the dependent variable (Table 3). The analysis gave a multiple regression coefficient of -.411 (p .05). The regression equation takes the form: $y = 24.7 - .717\ (\text{moisture stress} - 1.38\ [\text{soil temperature}])$.

Table 3. Linear correlation coefficient values for percent black knot disease (cm of gall/cm of stem) relative to independent environmental site factors.

Exposure	.110
Elevation	.287
Slope	.353
Soil pH	-.391
Soil depth	.151
Distance to surface H_2O	-.264
Plant moisture	-.439 (p = .065)
Soil temperature	-.440 (p = .055)
Percent understory cover	.101
Percent composition:	
a. Forbs	.215
b. Grasses	.061
c. Shrubs	.033
Average age of stand	-.086
Average height	-.002

Discussion and Conclusion

Koch (1935) and Smith (1970) found ascospore and conidia ejection occurred during rainfall, when the temperature was 10–15 C. Germination occurred when the relative humidity was 76%–90% and the temperature was between 12–30 C. Optimal germination occurred at 24 C. There is no information available on the environmental conditions necessary to maintain and increase fungal growth in vivo, although in vitro studies indicate 22–24 C as optimal for growth (Koch 1935). The environmental site factors found to be most closely correlated with disease incidence in this study were plant moisture stress and soil temperature. Low plant moisture stress reflects high moisture availability for both the plant and for the fungus. Soil temperature can exert strong influences on available soil moisture. Those sites with lower soil temperature and less plant moisture stress are probably the sites that receive and hold more spring moisture, which in turn would provide a more favorable site for infection. The results would suggest that the pathogen infects over the same range of elevation as chokecherry grows. Further studies are needed to establish the influence of the site factors we measured on those environmental factors that are necessary for fungal sporulation, dispersal, infection, and growth under field conditions.

Black knot is a disfiguring and debilitating disease on chokecherries. Knowledge of those site characteristics associated with high incidence of black knot can be useful in making management decisions concerning revegetation with chokecherry plants.

Literature Cited

Anderson, H. W. 1956. Diseases of fruit crops. McGraw-Hill, New York. 500 pp.

Beers, T. W., P. E. Dress, and L. C. Wensell. 1966. Aspect transformation in site productivity research. J. Forestry 64:691–692.

Koch, L. W. 1933. Investigations on black knot of plums and cherries I. Sci. Agr. 13:576–590.

______. 1934. Investigations on black knot of plums and cherries II. Sci. Agr. 15:80–95.

______. 1935a. Investigations on black knot of plums and cherries III. Sci. Agr. 15:729–744.

______. 1935b. Investigations on black knot of plums and cherries IV. Sci. Agr. 15:729–744.

Smith, D. H., F. H. Lewis, and S. H. Wainwright. 1970. Epidemiology of the black knot disease of plums. Phytopathology 60:1441–1444.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods, 6th ed. Iowa State University Press, Ames. 593 pp.

BIRDS OF THE DESERT REGION OF UINTAH COUNTY, UTAH

A. Gaylon Cook[1]

ABSTRACT.— The Common Loon, White Pelican, Double-crested Cormorant, recurvirostrids, and most grebes, waterfowl, gulls, and terns have become more abundant in Uintah County, Utah, since 1937 (Twomey 1942) due to the establishment of Pelican Lake and adjacent water bodies and the ponds and marshes at Ouray National Wildlife Refuge and Pariette Wetlands Wildlife Management Area. The incidence of herons, egrets, thrushes, nuthatches, and icterids has generally remained about the same since 1937. Diurnal raptors have largely declined in abundance in the desert region of Uintah County since Twomey's (1942) study. Plovers, sandpipers, phalaropes, and the White-faced Ibis were generally less common in 1977–1982 than in 1937, perhaps chiefly due to their displacement from wintering grounds by human population expansion and agricultural and industrial development. The incidence of owl species remains constant. Most flycatchers, swallows, warblers, vireos, orioles, and emberizids have diminished in number since 1937, probably because of the shrinkage of their winter habitats in Latin America and the southwestern U.S. The Blue Grosbeak and Black-throated Sparrow were not recorded in Uintah County in 1937 but were found there during this study and may represent a range extension northward since 1937. The Blue-gray Gnatcatcher is more common now than in 1937 due to the northward extension of its range. The Starling and Rock Dove and, more recently, the Common Grackle, Great-tailed Grackle, and Cattle Egret have invaded Uintah County due to the expansion of their ranges. It is not clear why the Pine Siskin, House Finch, and most corvids are presently less common than in 1937.

Description of the Desert Region of Uintah County

Uintah County, Utah (11,425 km^2), almost as large as Connecticut (12,973 km^2) and over twice as large as Delaware (5,328 km^2), is in northeastern Utah in the Colorado Plateau province (Breed 1976). I performed wildlife surveys on oil shale lands there from 1977 to 1982. Most observations included in this paper were made on lands or in the proximity of roads leading between oil shale leases and Vernal. Thus, this work is limited to sightings occurring in the lowlands of Uintah County. In this study, the desert region of Uintah County (principally at 1,400–1,675 m) includes desert scrub (or shrub, Graham 1937), desert-riparian (Fremont cottonwood—*Populus fremontii*, sandbar willow—*Salix exigua*, peach-leaf willow—*S. amygdaloides*, tamarix—*Tamarix pentandra* Pall, and box elder—*Acer negundo*; Graham 1937, Welsh and Moore 1973), and lowland pond, marsh, and lake habitats as well as agricultural and urban land. Plants along Green River at Split Mountain Campground in Dinosaur National Monument, including yellow willow (*Salix lutea*) and willow (*S. monticola*), are considered to constitute desert-riparian habitat although they exist in the transition zone between the latter and montane-riparian habitat. Vegetation along Ashley Creek at the mouth of Dry Fork Canyon (1830 m) and in and near Merkley Park (1830 m), consisting of thin-leaved alder—*Alder tenuifolia*, river birch—*Betula occidentalis*, narrowleaf cottonwood—*Populus angustifolia*, red osier dogwood—*Cornus stolonifera*, yellow willow—*Salix lutea*, willow—*Salix lasiandra* Benth., and bush honeysuckle—*Lonicera involucrata* (Graham 1937, Welsh and Moore 1973), is considered to be montane-riparian habitat. Juniper-pinyon woodlands in Uintah County are not considered to be part of its desert region.

GEOGRAPHIC LOCATIONS AND DATES OF AVIAN SIGHTINGS MADE BY OTHER OBSERVERS

Behle (1981) reviewed most of the ornithological work that occurred in the desert region of Uintah County. Other important avian studies there are reviewed as follows.

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C. Cottam observed birds near Jensen on 12 September 1941 (Hayward et al. 1976). Killpack and Hayward (1958, Hayward et al. 1976) watched birds approximately 18 km east of Jensen 9 June 1953, in the vicinity of Bonanza and Rainbow 16, 18, and 22 June 1954, about 13 km south of Ouray 29 May 1955, and at Pelican Lake 19 September 1956 and 17 June 1958.

Specimens were collected at Randlett 6 May 1950, 1 July 1957, and 22 July 1961, and at and near Jensen 19, 20, and 22 July 1937 and 18 May 1958; birds were seen along Green River near Ouray and south of Bonanza 17–18 May 1958 and near Randlett 13 May 1961 (Hayward 1967). From 1960 to 1970, C. L. Hayward, H. H. Frost, and associates (Hayward 1967, Hayward et al. 1976) made many avian observations at Pelican Lake.

Behle and Ghiselin (1958) collected birds about 5 km south of Vernal 26 July and 10 September 1948, 18 and 20 June 1949, and 6 and 25–27 August 1949, at Brush Creek, approximately 13 km northeast of Vernal, 24 August 1949, and about 5 km southwest of Jensen 27 July and 11 and 28 August 1949. Behle and Selander (1952) reported the capture of a Blue Grosbeak 5 km south of Vernal in June 1950 and the observation of the species at Vernal 4 August 1951. G. Lloyd and C. M. White made observations and collected specimens along the White River west of Ouray in July 1961 as part of the larger study of Utah by Behle (White, pers. comm.).

M. A. Strong (Olsen 1973) surveyed birds in the oil shale area of Uintah County in 1972 and 1973 and performed breeding bird inventories there in spring 1973. Ornithologists on the White River Project Team surveyed birds on and near the federal oil shale tracts U-a and U-b southwest of Bonanza in 1975 and 1976 (Anonymous 1977). Sangster (1976, 1977) performed avian studies at Ouray National Wildlife Refuge (ONWR) and Pelican Lake in the spring of 1975 and 1976. At Kennedy Basin 18 km northwest of Bonanza, B. H. Green (1981) and A. R. Johnson (1981) studied habitat utilization among Sage Sparrows and Lark Buntings, respectively, in 1979 and 1980. In recent years, several birders, including E. Sorenson, R. Sorenson, M. L. Perry, and M. Webb, have reported unusual sightings of birds in Uintah County to *American Birds*. D. Chure and L. Ferris and other personnel with the U.S. National Park Service, T. Tornow, M. Lange, and H. G. Troester, personnel with the U.S. Fish and Wildlife Service, and D. Zalunardo, S. Madsen, and K. L. Parr, employees of the Bureau of Land Management, provided many sighting records at Dinosaur National Monument, ONWR, and Pariette Wetlands Wildlife Management Area (PWA), respectively. J. S. Cranney and M. Schwinn, employees of the Utah State Division of Wildlife Resources, supplied the locations of several raptor nesting sites in the desert region of Uintah County, and M. Horton and P. Wagner made raptor observations there. Utah Field Ornithologists visited ONWR, Pelican Lake, Stewart Lake Wildlife Management Area (SLWMA), Dinosaur National Monument, and Vernal City parks 15–16 May 1982. D. Chure, L. Ferris, M. S. Fisher, J. Harris, M. Lange, A. Leppert, C. Leppert, M. Leppert, P. Leppert, and R. Mackin performed an Audubon Christmas bird count in the Jensen area 26 December 1982 (D. Chure and L. Ferris, pers. comm.).

METHODS

This paper does not include all avian observations that have been made in the desert region of Uintah County, Utah. It indicates sightings or collections of the author and other ornithologists or birders demonstrating the relative abundance or periods of occurrence of species in that region different from that reported in one or more published works cited here.

The incidence of birds in Twomey's (1942) study and mine (Fig. 2) are often compared. In designating the relative abundance of species in 1934, 1935, and 1937 versus 1977–1982, the same criteria were not used because A. C. Lloyd's investigation continued for only 36 days in spring and summer 1934 and four months in spring and summer 1935 (Twomey 1942), and Twomey's (1942) study lasted only five months in 1937 whereas my investigation continued for five years.

A species was considered rare when from 1 to 3 separate sightings were made of fewer than 5 individuals or when only one sighting was made of a flock of 5 or more individuals. For Twomey's (1942) study, uncommon species generally include those that were noted as being rare, uncommon, not plentiful, not abundant, not numerous, or as being represented by few individuals. When the number of bird observations was recorded, a species was regarded as uncommon when 4–24 sightings were made of fewer than 5 individuals or when 2–14 sightings were made of flocks comprising 5 or more individuals. In this study, a species was considered uncommon when fewer than 5 representatives were observed on 4–24 different days or when 5 or more individuals were sighted on 2–19 different days.

For Twomey's investigation, common species generally include those that were indicated as being common, plentiful, numerous, abundant, frequently seen, or seen in considerable numbers. When bird observations were enumerated, species were usually considered common when 25 or more sightings were made of fewer than 5 individuals or when 15 or more sightings were made of flocks consisting of 5 or more individuals. In the present study, species were considered common when fewer than 5 individuals were sighted on 25–100 different days or when flocks of 5 or more individuals were observed on 20–50 days. Species recorded in Twomey's study are regarded as abundant when they were noted as being very abundant, very plentiful, very numerous, very common, or the most abundant or widely distributed bird in one type of habitat. In this investigation, a species was considered abundant when fewer than 5 representatives were observed on 100 or more different days or when flocks of 5 or more individuals were observed on 50 or more different days.

The sites of my observations are shown in Figure 1 and the periods during which different species were sighted are indicated in Figure 2. In this paper, common names and scientific taxonomic nomenclature and the sequence of species presentation are according to the American Ornithologists' Union (1982).

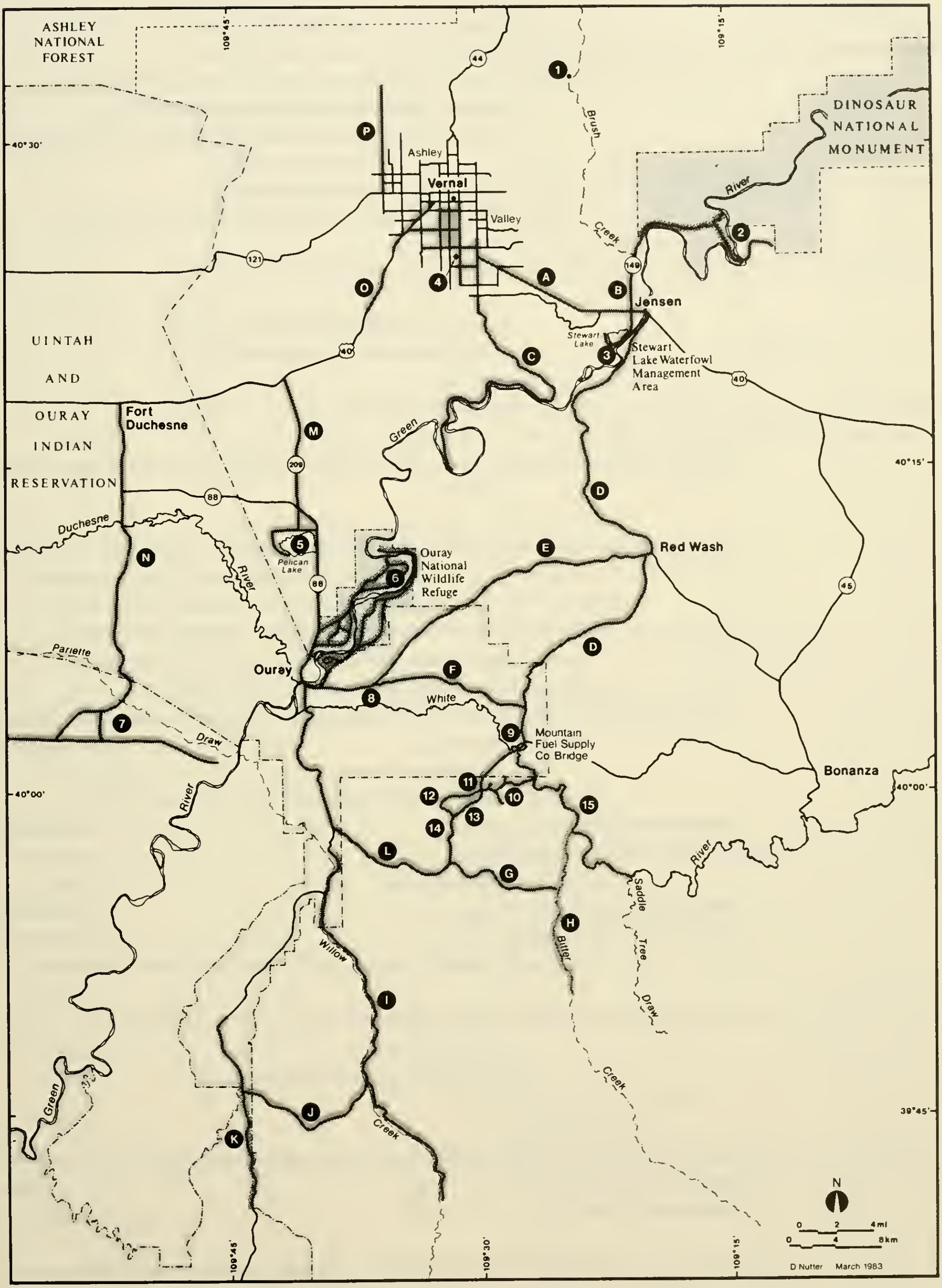
OBSERVATIONS AND DISCUSSION

Gaviiformes

Gaviidae

Common Loon (*Gavia immer*). Most sightings occurred during migration in April, May, and September at Pelican Lake (Twomey 1942, Hayward et al. 1976, Sangster 1976, Leppert 1982, Fig. 2) and Bottle Hollow Resort (S. Madsen, pers. comm.). M. Lange, D. Chure, and L. Ferris saw two birds at Bottle Hollow Resort 4 July 1982

Fig. 1. Map of the desert region of Uintah County, Utah showing the routes and areas where the author made avian observations in 1977–1982: 1, Glade Holmes Ranch along Brush Creek 16 km northeast of Vernal. 2, Southwestern part of Dinosaur National Monument, Utah, and environs. 3, Stewart Lake Waterfowl Management Area. 4, Ashley Valley, particularly the author's backyard in Naples. 5, Pelican Lake and environs, including ponds to the east and west. 6, Ouray National Wildlife Refuge. 7, Pariette Wetlands Wildlife Management Area. 8, Cottonwood Grove north of the White River, 7 km southeast of Ouray. 9, Area in vicinity of Mountain Fuel Supply Company bridge on the White River. 10, Sand Wash and roads in its vicinity. 11, Area at 40°00′N, 109°31′W. 12, Interspersed Black Sagebrush and Spiny Hopsage–Shadscale–Horsebrush communities and a pond at 40°00′N, 109°32′W. 13, Mixed desert scrub community in sand dunes at 39°59′N, 109°31′W. 14, Wash with vegetation dominated by greasewood and environs of that wash at 39°57 to 58′N, 109°32′W. 15, White River between West Fork of Saddle Tree Draw and Mountain Fuel Supply Company bridge. A, U.S. Highway 40 between Vernal and Jensen. B, Utah State Highway 149 between Stewart Lake Waterfowl Management Area and Dinosaur National Monument. C, Route extending from the intersection of Roads 1500 East and 5000 South, south of Naples, to Horseshoe Bend of the Green River. D, Road extending from Green River bridge at Jensen to Mountain Fuel Supply Company White River bridge via Red Wash. E, Glen Bench Road extending from Red Wash Road to the southern Ouray-Bonanza Road. F, Road extending from Green River bridge at Ouray to Road D. G, Road extending to the Bitter Creek Basin from junction of road proceeding to Mountain Fuel Supply Company bridge and road proceeding to Ouray via Seep Ridge Road. H, Road in Bitter Creek Basin continuing from confluence of Bitter Creek and White River south for 16 km. I, Road along Willow Creek. J, Road passing through Green Canyon between Willow Creek and Hill Creek. K, Road along Hill Creek. L, Road extending to Seep Ridge Road and thence to Ouray from junction of road proceeding to Mountain Fuel Supply Company bridge and road proceeding to Bitter Creek Basin. M, Road extending from U.S. Highway 40 to Ouray via Utah Highways 209 and 88. N, Road extending from U.S. Highway 40 south to Pariette Wetlands Wildlife Management Area via Fort Duchesne. O, Section of U.S. Highway 40 southwest of Asphalt Ridge.


ASHLEY NATIONAL FOREST
DINOSAUR NATIONAL MONUMENT
UINTAH AND OURAY INDIAN RESERVATION
Fort Duchesne
Ashley
Vernal
Valley
Jensen
Stewart Lake
Stewart Lake Waterfowl Management Area
Brush Creek
River
Green
Red Wash
Pelican Lake
Ouray National Wildlife Refuge
Ouray
Duchesne River
Pariette Draw
White
Mountain Fuel Supply Co Bridge
Bonanza
River
Saddle Tree Draw
Bitter Creek
Willow Creek
Green River
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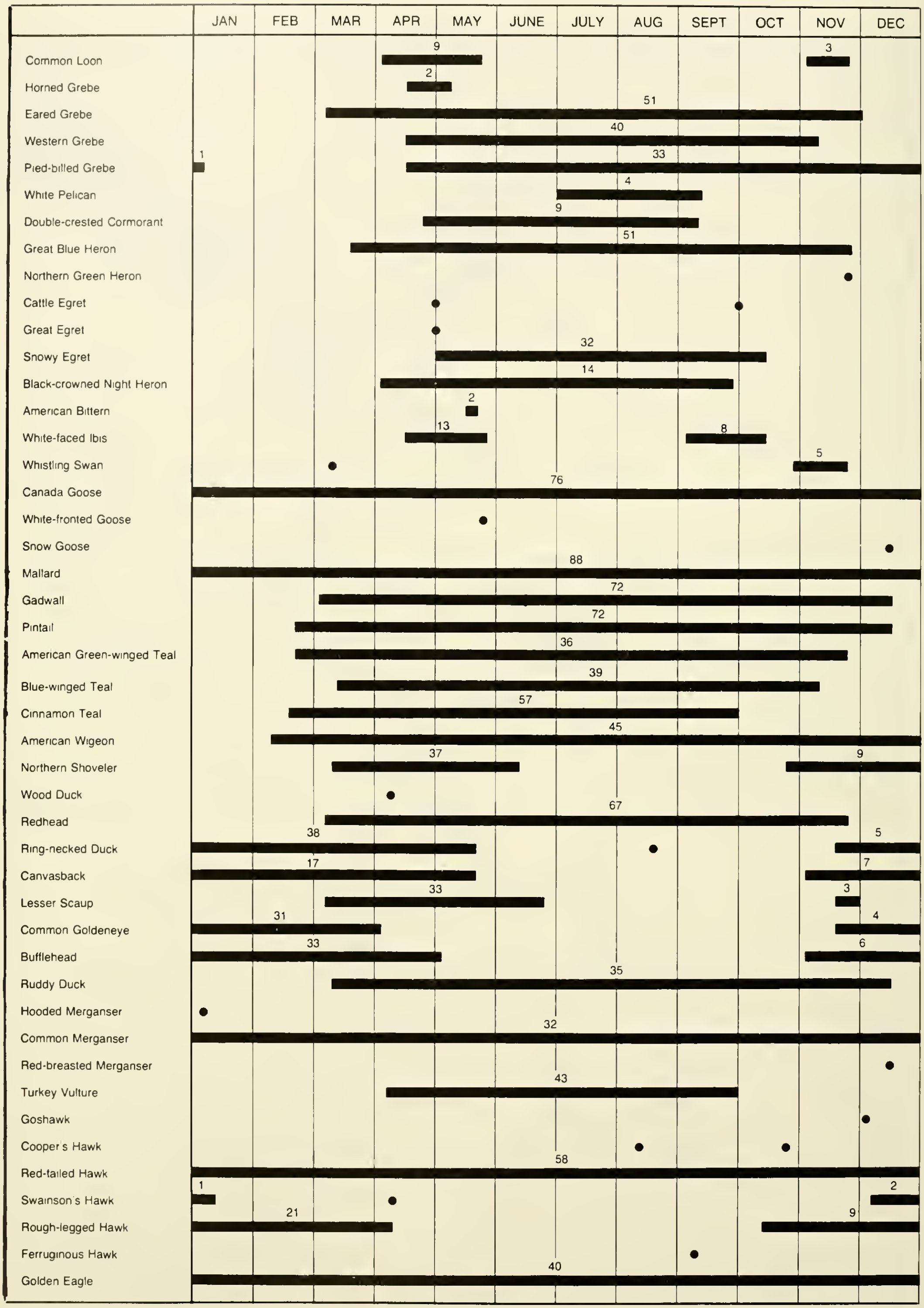


Fig. 2. Periods of avian occurrence and number of different days that bird species were observed in this study. Figure 2 was completed before the latest check-list of North American birds was published by the American Ornithologists' Union (1982). The nomenclature and sequence of species listed in Figure 2 are according to Hayward et al. (1976).

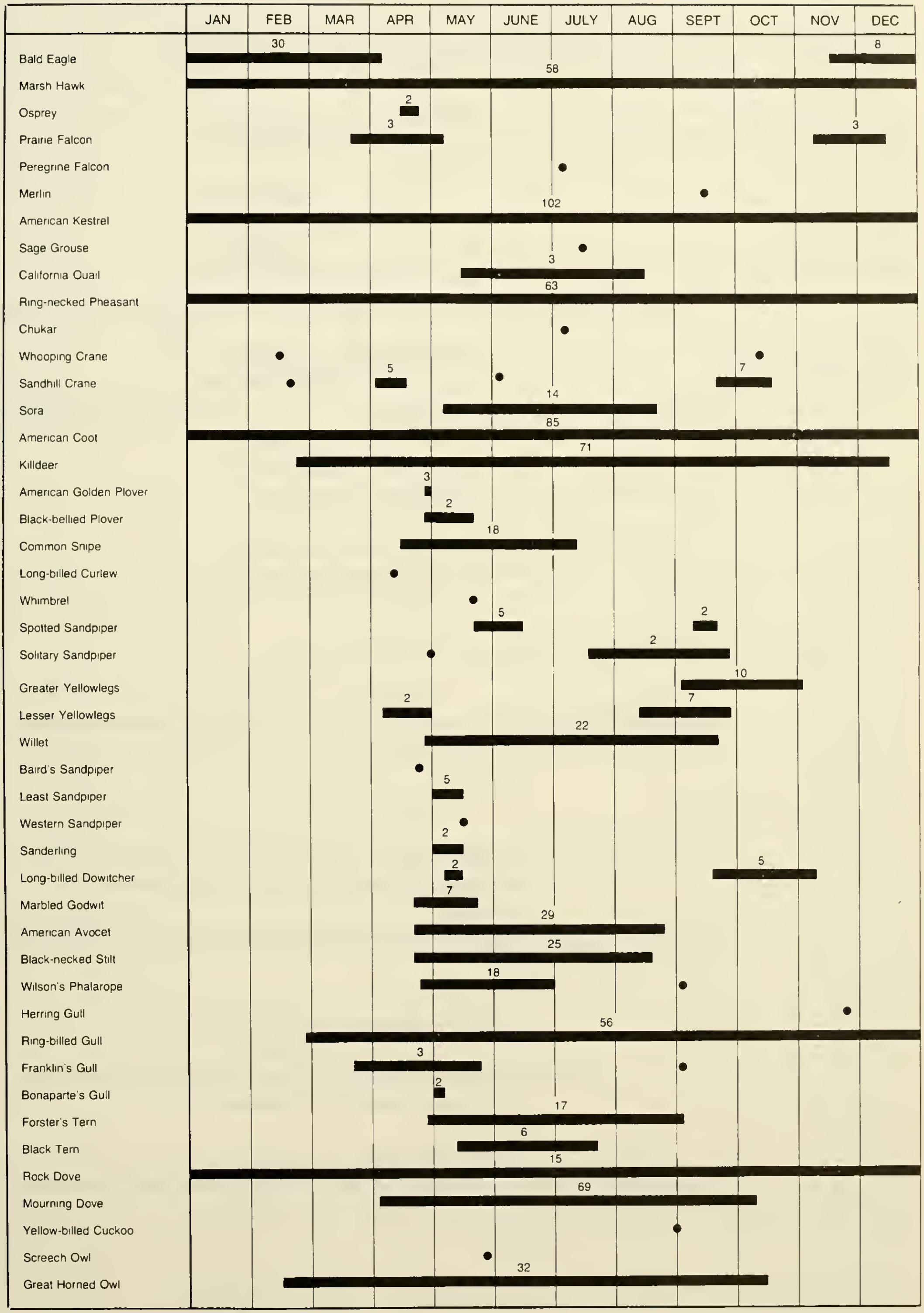


Fig. 2b (continued).

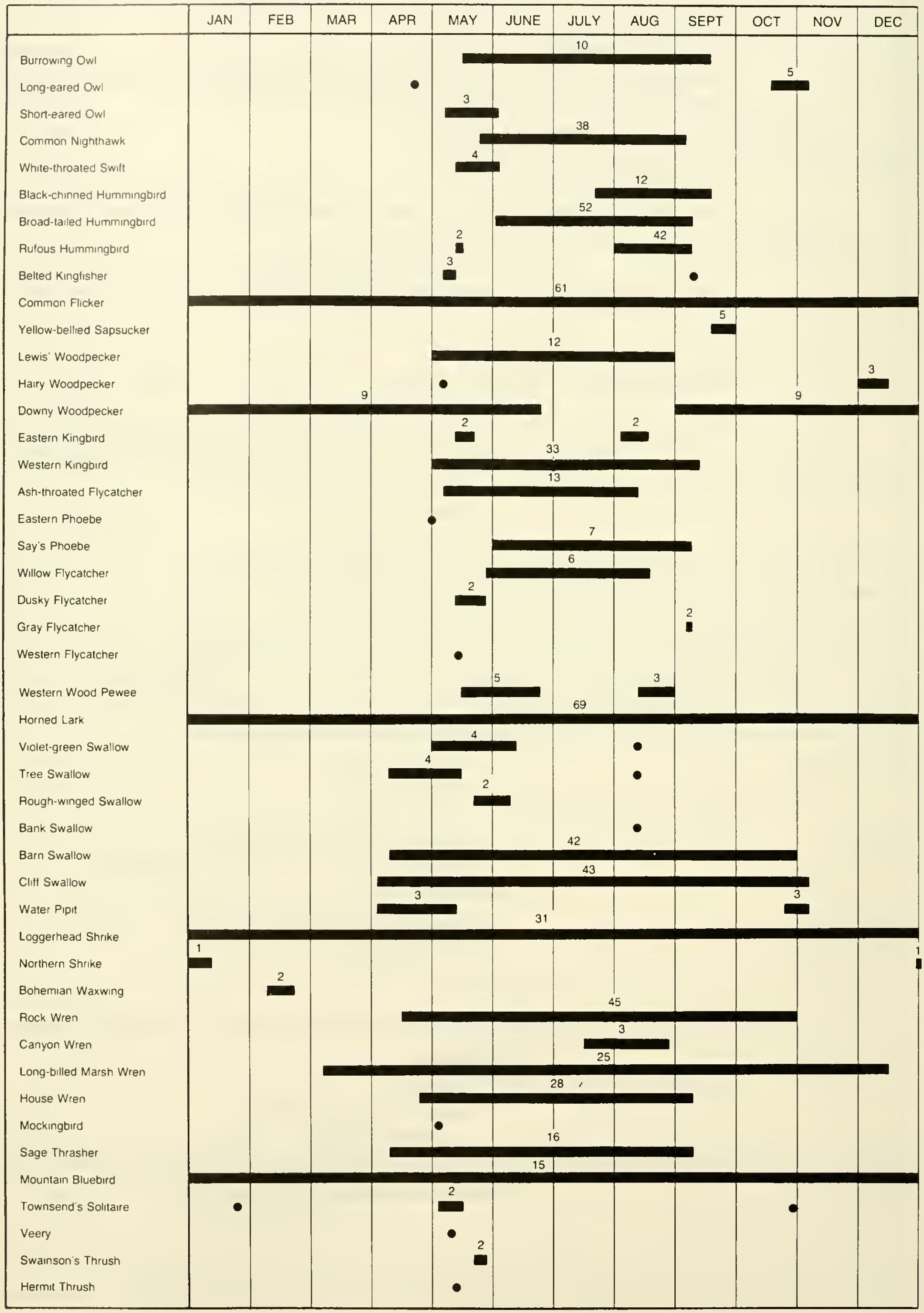


Fig. 2c (continued).

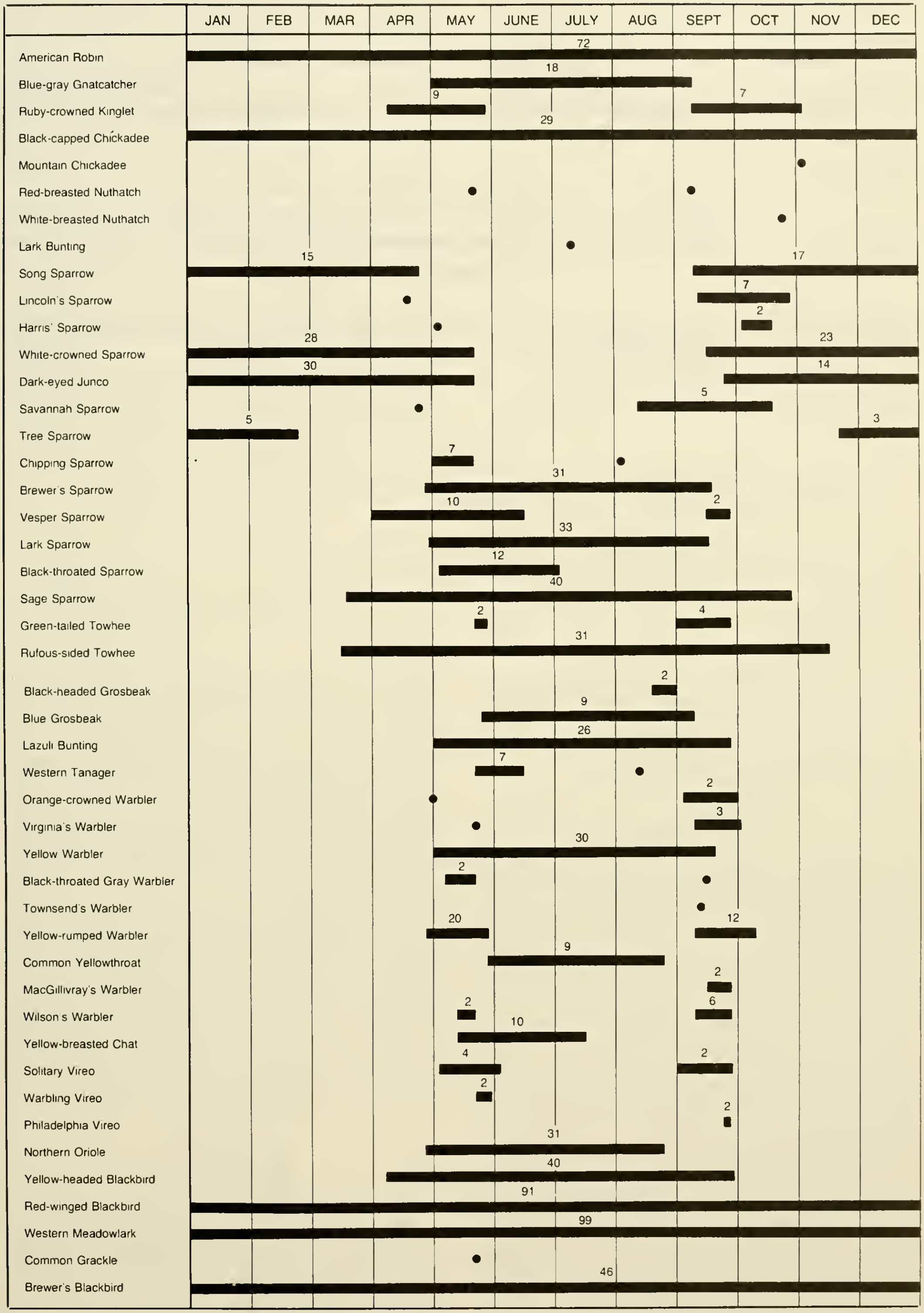
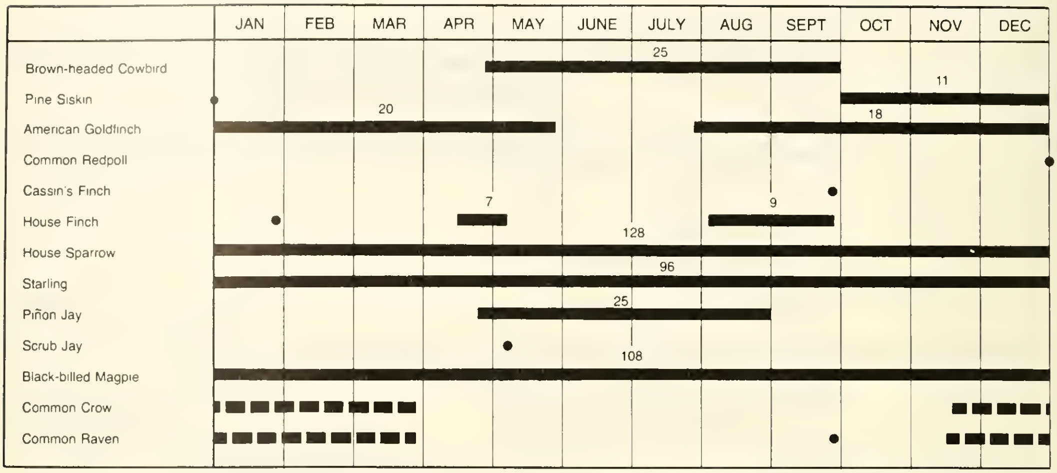


Fig. 2d (continued).



LEGEND

▬ 9 Bar shows time period during which a species was observed. Number above bar indicates the number of different days that the species was seen.

● Indicates a single day of observation of a species in a season.

■■■ Shows that a species was seen during a time period although no specific sighting date is available.

Fig. 2e (continued).

(D. Chure, pers. comm.), and E. Sorenson and R. Sorenson saw four birds in the Vernal area 7 July 1981 (Kingery 1981d). I observed the species as late as November (Fig. 2).

Podicipedidae

Pied-billed Grebe (*Podilymbus podiceps*). More common than in 1937 (Twomey 1942) due to the creation of Pelican Lake and ponds at ONWR and PWA. Young were observed in the present study at the permanent pond east and across Utah Highway 88 from Pelican Lake (Fig. 1) 16 July 1981. The commonly occurring species of grebes in Uintah County do not overwinter there (Fig. 2) as they do in some parts of Utah (Hayward et al. 1976).

Horned Grebe (*Podiceps auritus*). At ONWR, one bird was observed by L. Malone (Kingery 1980a) 11 March 1980. I saw one individual at the front (west) pond of ONWR and the pond 1 km west of Pelican Lake (Figs. 1–2). On 15–16 May 1982, Utah Field Ornithologists sighted 2 individuals at Pelican Lake and a total of 10 birds in the Uinta Basin (Leppert 1982). N. Howk (D. Chure, in litt.) saw 2 birds in winter plumage on Green River at Dinosaur National Monument 28 August 1982.

Eared Grebe (*Podiceps nigricollis*). These have increased numerically (Fig. 2) since 1937 (Twomey 1942). A colony of more than 50 nested at Woods Bottom of ONWR in 1981 and 1982 (T. Tornow and H. G. Troester, pers. comm.).

Western Grebe (*Aechmophorus occidentalis*). Recorded as a migrant in 1937 (Twomey 1942). At least 13 sightings of the species in addition to mine (Fig. 2) were made from 18 April–19 September in 1956, 1961, 1963, 1964, 1966, 1967, 1981, and 1982 (Hayward 1967, Behle 1981, Leppert 1982, D. Chure and L. Ferris, pers. comm.).

Pelecaniformes

Pelecanidae

American White Pelican (*Pelecanus erythrorhynchos*). A few birds were seen in May 1937–1963 (Twomey 1942, Hayward 1966, Hayward 1967, D. Chure, in litt.). At ONWR, White Pelicans were seen 15 September–13 November 1980, 10–24 April

1981 (38 birds), and 23 June 1981 (43 individuals; Kingery 1981a, T. Tornow, pers. comm.). In April 1981, the bill of some males bore a protuberance suggesting that they were already in breeding condition as they migrated northward (T. Tornow, pers. comm.). The Utah Department of Natural Resources, Division of Wildlife Resources (Kingery 1981d) noted that 40–50 nonbreeding individuals summered in the Vernal area in 1981 when over 50 were seen simultaneously at the desiltation pond of PWA, where they remained throughout the summer (K. L. Parr and D. Zalunardo, pers. comm., Fig. 2). D. Chure and L. Ferris (pers. comm.) sighted 3 (2 with a protuberance of the bill) at SLWMA 18–19 April 1982. I observed one individual twice at Pelican Lake and twice at Woods Bottom Pond of ONWR (Fig. 2).

Phalacrocoracidae

Double-crested Cormorant (*Phalacrocorax auritus*). More abundant than in 1937 (Twomey 1942) due to the creation of a pond with cottonwood snags in its center approximately 1 km west of Pelican Lake and the establishment of ponds and marshes at PWA and ONWR (Fig. 1). At the rookery west of Pelican Lake, R. Sorenson and E. Sorenson (Kingery 1981c) observed 10 occupied nests 2 May 1981 and 18 such nests 27 June 1981. Utah Field Ornithologists saw 53 birds there and 3 at ONWR 15–16 May 1982 (Leppert 1982). At PWA, I observed immature individuals 30 June and 3 adults 7 July 1981 (Fig. 2). I sighted the species at ONWR, Pelican Lake, and the rookery 1 km west of Pelican Lake, where I observed 34 individuals on nests 24 April and 42–50 birds 1, 7, 14, and 21 May 1982 (Fig. 2).

Ciconiiformes

Ardeidae

Least Bittern (*Ixobrychus exilis*). One seen at ONWR by T. Tornow (pers. comm.) in the spring of 1979 and 1981 and by H. G. Troester (pers. comm.) in summer 1982. The species was also observed by M. Bromley at Jensen (presumably at SLWMA) in May 1983 (Kingery 1983).

Great Egret (*Casmerodius albus*). Seen in the Jensen area in May and September (Twomey 1942, D. Chure, in litt.). D. Chure and L. Ferris (pers. comm.) observed one bird at the pond 1 km west of Pelican Lake 25 April 1981. I saw one individual 1 May 1982 approximately 30 m away from a Great Blue Heron at the northwest end of the pond 1 km west of Pelican Lake (Figs. 1–2).

Little Blue Heron (*Egretta caerulea*). Seen at ONWR in May 1981 (H. G. Troester, pers. comm.).

Cattle Egret (*Bubulcus ibis*). H. G. Troester (pers. comm., Behle 1981) observed one along Ashley Creek about 3 km northwest of Vernal 1 November 1978. It was also seen in the Vernal area in spring 1981 (Kingery 1981c). I observed two at and near the diked marsh located at the northwest end of Pelican Lake and 17 in a pasture at site 4 (Figs. 1–2).

Green-backed Heron (*Butorides striatus*). Sighted in fall 1978 (Kingery 1979a, Behle 1981) and observed at ONWR in spring 1981 (H. Troester, pers. comm.). Both adults and immatures were observed there 24 July 1981 (T. Tornow, pers. comm.). I saw one at Woods Bottom Pond of ONWR (Figs. 1–2).

Threskiornithidae

White-faced Ibis (*Plegadis chihi*). At ONWR, 50 nests were found in 1979, 160 birds were seen 12–14 May 1981, and 31 birds were observed 23–24 July 1981 (T. Tornow, pers. comm.). In both 1980 and 1981, it appeared to nest at ONWR (T. Tornow, pers. comm.). I sighted it on 21 different days (Fig. 2).

Anseriformes

Anatidae

Greater White-fronted Goose (*Anser albifrons*). I observed one at ONWR with a flock of Canada Geese (*Branta canadensis*) 24 May 1978 (Fig. 2).

Snow Goose (*Chen caerulescens*). Seen at Stewart Lake 28 October 1957 (Hayward 1967), PWA in mid-November (D. Zalunardo, pers. comm.), ONWR 21 May 1966 (Behle 1981) and November 1982 when 9 were sighted (H. G. Troester, pers. comm.), and at Pelican Lake 14 March 1975 (17 birds—Sangster 1977) and 16 December 1981 (1 bird—Fig. 2).

Ross' Goose (*Chen rossii*). Reportedly observed at ONWR in spring 1981 (T. Tornow, pers. comm.).

Wood Duck (*Aix sponsa*). T. Tornow (pers. comm.) observed it at ONWR 7 October 1980. At PWA, a male was seen 15 October 1981 and a female was observed during the first week of November 1981 (K. L. Parr and D. Zalunardo, pers. comm.). H. G. Vickers, an associate of the author, observed one in the marsh at the southeast end of Pelican Lake 6 April 1982 (Fig. 2). R. Sjostrom (M. Lange, pers. comm.) saw three individuals in early October 1982.

Green-winged Teal (*Anas crecca*). Regarded by Behle (1981) as an uncommon summer resident and an occasional winter visitant in northeastern Utah. It is now a common migrant and spring, summer, and fall resident (a species was considered to be a fall resident when it was sighted from late September through most or all of November) in Uintah County (Fig. 2).

The **Mallard** (*Anas platyrhynchos*), **Northern Pintail** (*Anas acuta*), and **Gadwall** (*Anas stepera*) are presently abundant in Uintah County (Fig. 2) and are more plentiful now than in 1937 (Twomey 1942) due to the establishment of Pelican Lake and the marshes at ONWR and PWA. Northern Pintails and Gadwalls are common nesters at PWA (D. Zalundardo, pers. comm.). Gadwalls have not been seen in Uintah County in January and February, but Killpack (1959) observed four on 29 December 1958. I did not see Northern Pintails from 16 December to 19 February (Fig. 2).

Blue-winged Teal (*Anas discors*). Considered by Behle (1981) to be uncommon breeders in northeastern Utah. They are presently common spring and summer residents and migrants in Uintah County (Fig. 2).

Cinnamon Teal (*Anas cyanoptera*). Presently a common spring and summer resident and migrant in Uintah County (Fig. 2).

Eurasian Wigeon (*Anas penelope*). One observed at PWA in April 1979 (D. Zalundardo, pers. comm.).

American Wigeon (*Anas americana*). Considered to be rare in northern Utah (Behle and Perry 1975a) and less than common (occasional breeder) in northeastern Utah (Behle 1981) during summer. I found it to be a common migrant and spring, summer, and fall resident in Uintah County (Fig. 2).

Canvasback (*Aythya valisineria*). Although previously reported as uncommon (Hayward 1967, Behle and Perry 1975a, Behle 1981), Canvasbacks are now common migrants and winter residents (Fig. 2). A Canvasback brood of two was seen at ONWR in 1980 and a hen was observed there 16 July 1981 (T. Tornow, pers. comm.).

Redhead (*Aythya americana*). Although formerly considered a hypothetical breeder (Hayward 1967, Behle 1981), it is now abundant in Uintah County except in winter (Fig. 2).

Ring-necked Duck (*Aythya collaris*). Considered to be a casual (Hayward et al. 1976) or uncommon (Behle and Perry 1975a) migrant, occasional winter visitant (Behle and Perry 1975a), and rare summer resident (Hayward et al. 1976) in Utah. In Colorado, the species is a regular migrant and an uncommon summer resident (Bailey and Niedrach 1965). Ring-necked Ducks, now common, arrive in Uintah County at about the same time that Common Goldeneyes do in fall but remain there longer in spring (Fig. 2). They are most prevalent from March to May. In 1981 at the west pond of ONWR, T. Tornow (pers. comm.) saw a male 23 July and I observed one 18 August (Fig. 2).

Lesser Scaup (*Aythya affinis*). Regarded as rare (Behle and Perry 1975a) or uncommon (Hayward et al. 1976) breeders in northern Utah or nonbreeders in northeastern Utah (Behle 1981). It nested at ONWR in 1979 and 1980 (T. Tornow, pers. comm.) and at PWA in July 1981. At Pelican Lake, it is common in spring and scarce in fall (Fig. 2).

Common Goldeneye (*Bucephala clangula*). Regarded by Behle and Perry (1975a) and Behle (1981) as an uncommon migrant and winter visitant in Utah and northeastern Utah, respectively. It is a common winter resident (Fig. 2).

Barrow's Goldeneye (*Bucephala islandica*). A male was reported by J. M. Good (Beidleman, in litt.) at the bend of the Green River northeast of Escalante's Crossing near the southwest entrance to Dinosaur National Monument 29 February 1956.

Bufflehead (*Bucephala albeola*). Considered to be an uncommon migrant but not winter resident in northeastern Utah (Behle 1981). In Uintah County, it is now also a common winter resident and is more frequently seen in spring than fall (Fig. 2).

Hooded Merganser (*Lophodytes cucullatus*). A male and female were seen at ONWR 6 March 1981 (T. Tornow, pers. comm.). The species was reported at PWA in spring 1981 (K. L. Parr, pers. comm.). I observed several on a stream in SLWMA 6 January 1982 (Fig. 2).

Common Merganser (*Mergus merganser*). Twomey's (1942) study extended from 1 May to 30 September 1937 and he did not see the species in Uintah County. Sightings there are from February to the first week of June 1966, 1967, 1975, 1976, 1980, and 1982 (Anonymous 1977, Sangster 1977, Behle 1981, Leppert 1982, T. Tornow, pers. comm.). In the Roosevelt area (including part of western Uintah County), Common Mergansers were seen in December 1953, 1954, and 1956–58 (Crittenden et al. 1955, Killpack 1957, 1958, 1959, Killpack et al. 1954). In the Jensen area, 13 were seen 26 December 1982 (D. Chure and L. Ferris, pers. comm.). I observed the species every month except June and September (Fig. 2) and saw large flocks on Pelican Lake in winter, particularly in March. It is a common permanent resident (Fig. 2).

Red-breasted Merganser (*Mergus serrator*). Frequented the Green River floodplain in early May and late September 1937, when one to five individuals were observed feeding on that river or Stewart Lake nearly every day (Twomey 1942). Since then, it has been less common. Hayward (1967) observed it on Green River near Ouray 18 May 1958. S. Madsen (pers. comm.) saw three males and two females at Bottle Hollow Resort 19 April 1980. The species was seen at PWA in spring 1981 (D. Zalunardo and K. L. Parr, pers. comm.) and at Pelican Lake 16 December 1981 (Fig. 2). T. Tornow (pers. comm.) observed it at the pond near the west entrance to ONWR in spring 1982.

Ruddy Duck (*Oxyura jamaicensis*). Although considered a common migrant and rare winter resident in northeastern Utah (Behle 1981), I observed it throughout the summer (Fig. 2) and sighted young at Pelican Lake 16 July 1981. The latest sighting in Uintah County or eastern Duchesne County during winter was 29 December (Killpack et al. 1956). The species is a common spring, summer, and fall resident (Fig. 2).

Falconiformes

Accipitridae

Osprey (*Pandion haliaetus*). One bird was sighted at SLWMA 1 km beyond its entrance 28 April 1975 by S. Baese, R. King, and B. King (D. Chure, in litt.). According to D. B. Beard (Beidleman, in litt.), Ranger Baldwin of Dinosaur National Monument observed Ospreys nesting at Split Mountain (probably not in the desert region of Uintah County) about 1936–1937. Twice I saw one in a cottonwood tree southwest of Pelican Lake (Fig. 2). Perhaps that was the bird seen at the pond 1 km west of Pelican Lake 1 May 1982 by D. Chure, L. Ferris, M. Lange, and N. Howk (D. Chure, pers. comm.). The above sightings may have been of birds that breed at Flaming Gorge Reservoir, where there were six nesting pairs in 1979 and 1980 according to P. Wagner (Kingery 1980b). Other sightings have been reported by Twomey (1942), Hayward (1967), and Behle (1981).

Bald Eagle (*Haliaeetus leucocephalus*). In Uintah County, more than 21 sightings were made from 27 November to 26 February 1954, 1966, 1967, 1974, 1975, 1977, and 1982 (Behle and Perry 1975b, Behle 1981, D. Chure and L. Ferris, pers. comm.). I observed it on 38 different days (Fig. 2). In early January, personnel of the U.S. Department of Interior, Bureau of Land Management, flew over the Green River from Split Mountain, Dinosaur National Monument, to Sand Wash (in Uintah and western Duchesne counties) and counted 22 birds in 1980, 33 in 1981, and 45 in 1982 (S. Madsen, pers. comm.). At ONWR, 52 were seen at Woods Bottom in February 1982 (T. Tornow, pers. comm.) and/or 7 March 1982 (M. Lange, pers. comm.).

Northern Harrier (*Circus cyaneus*). Hayward et al. (1976) noted that few remain in lower valleys of Utah in winter. In Uintah County I observed as many in winter as in summer (Fig. 2). Many other winter observations have been made there (Crittenden et al. 1953, 1955, Killpack 1957, 1958, 1959, Killpack et al. 1952, 1954, 1956, Behle 1981).

Sharp-shinned Hawk (*Accipiter striatus*). Considered by Behle and Perry (1975a), Hayward et al. (1976), Behle (1981), and Twomey (1942) to be common in desert-riparian habitat as well as montane forests in Utah. In Colorado, it is reportedly uncommon (Bailey and Niedrach 1965). I did not observe it. In what was possibly the desert region of Dinosaur National Monument, one was seen south of Josie Morris Cabin by B. Ingber 9 July 1980, in the "Frontier Formation" by J. Freilich 13 September 1978, in Orchid Draw west of Dinosaur Quarry Visitor Center by W. Truesdell 10 September 1973, and "Shinarrump Hogback" 200 m west of Split Mountain Campground by D. Thompson 10 January 1966 (D. Chure, in litt.). One was seen at the Jensen refuse site by D. Chure and L. Ferris (pers. comm.) 28 November 1982.

Cooper's Hawk (*Accipiter cooperii*). In the desert region of Uintah County, it has been seen on at least 29 occasions from 12 April to 31 [sic] September 1948, 1966, 1971, 1974, 1975, and 1978–1982 (Behle and Perry 1975b, Behle 1981, Leppert 1982, D. Chure, in litt., Fig. 2), but 20 of those observations occurred in or adjacent to Dinosaur National Monument (D. Chure, in litt., Fig. 2). It nested along White River in 1975 (Behle 1981) and 400 m from the Dinosaur Quarry Visitor Center in 1981 and 1982 (D. Chure and L. Ferris, pers. comm.). Presently two nests occur at T3S, R20E, T3S, R21E, and T3S, R25E and one each at T3S, R23E, T3S, 22E, T2S, R22E, T4S, R22E, T10S, R24E, and T9S, R26E (J. S. Cranney, pers. comm.).

Northern Goshawk (*Accipiter gentilis*). One seen along Seep Ridge Road 32 km south of Ouray 29 September 1974 (Behle 1981). I observed one on a bluff in badlands near Sand Wash at site 10 (Figs. 1–2). D. Chure and L. Ferris (pers. comm.) observed another at Jensen 16 December 1980. The species was seen at PWA 11 and 19 February 1981 (D. Zalunardo and K. L. Parr, pers. comm.). M. Horton and S. Madsen (S. Madsen, pers. comm.) saw one in cottonwoods along Deep Creek approximately 1.5 km north of Lapoint (possibly in the desert region of Uintah County) 10 December 1981. Utah Field Ornithologists sighted one at Josie Morris Cabin, Dinosaur National Monument 15 May 1982 (Leppert 1982). In Uintah County, it has not been observed to nest in valleys (J. S. Cranney, in litt.) as it did on a Yampa River floodplain in Moffat County, Colorado, 800 m east of the eastern boundary of Dinosaur National Park (White et al. 1965).

Broad-winged Hawk (*Buteo platypterus*). Reported at "Dinosaur, Utah" (presumably Dinosaur National Monument, Utah) between 1 March and 31 May 1982 by J. Burns and M. Webb (Kingery 1982). Utah Field Ornithologists saw one immature at Josie Morris Cabin, Dinosaur National Monument, 15 May 1982 (Leppert 1982), not 5 May 1982 as reported by White et al. (1983). Nine Utah sightings have been reported (Kingery 1983).

Swainson's Hawk (*Buteo swainsoni*). Reported to be present in Utah from 22 March to 10 November (Behle and Perry 1975a), occasional in Utah during winter (Hayward et al. 1976), or rare in the Uinta Basin then (Behle 1981). It is the most abundant buteo in Colorado, where it is common in summer, abundant in migration, and rare in winter (Bailey and Niedrach 1965).

In Dinosaur National Monument, one was observed by E. Sorenson and R. Sorenson 21 February 1981 (Kingery 1981b), at a pump immediately southwest of Josie Morris Cabin by B. Ingber 11 June 1980 (D. Chure, in litt.), and at Green River Campground by N. Stephan 21 August 1973 (D. Chure, in litt.). Crittenden et al. (1953) saw one in the Roosevelt area (including part of western Uintah County) 23 December 1952. The species was observed at Dragon (possibly in the desert region of Uintah County) 4 September 1974 (Behle 1981). I observed one immature and one adult near Pelican Lake, one adult in Vernal and at site 4, and a flock of 4 in desert scrub habitat at 39°59′N, 109°30′W near the western end of the major road at site 10 (Figs. 1–2). Utah Field Ornithologists sighted 2 at Pelican Lake and 11 in the Ouray area 15–16 May 1982 (Leppert 1982, D. Chure, pers. comm.). Two nests were found at T7S, R25E, Sec. 21 (J. S. Cranney, pers. comm.). The species' numbers have apparently declined since 1937 (Twomey 1942).

Ferruginous Hawk (*Buteo regalis*). Reported as rare (Behle and Perry 1975a) or seldom seen (Hayward et al. 1976) in Utah during winter. In an area including part of western Uintah County, one was seen in late December 1951–1953 and 1958 (Crittenden et al. 1953, Killpack 1959, Killpack et al. 1952, 1954). At ONWR, M. Lange (pers. comm.) saw one several times throughout the winter of 1981–1982 and Utah Field Ornithologists sighted a raptor they believed was a Ferruginous Hawk 15 or 16 May 1982 (Leppert 1982, M. Lange, pers. comm.). W. H. Dines (D. Chure, in litt.) observed one near the Escalante Ranch House south of southwestern Dinosaur National Monument 31 July 1981. J. Metz and I sighted one along a road 1.5 km southwest of MFB (site 9) 9 September 1981 (Figs. 1–2). Ferruginous Hawks are believed to nest at PWA, where they were observed during the nonbreeding season from early November 1980 to 6 January 1981 (D. Zalunardo and K. L. Parr, pers. comm.). In 1981 and 1982, personnel with the Utah Division of Wildlife Resources (J. S. Cranney, pers. comm.) found 14 nests 3.0–14.5 km west of the Utah-Colorado border (40°06 to 09′N, 109°05 to 13′ W). Three of them were active in both 1981, and four (not necessarily the same ones) were active in 1982 (J. S. Cranney, pers. comm.). The present distribution of the species in Uintah County is localized. During a two-hour period on 5 May 1937, Twomey (1942) observed 40 birds spaced approximately 1.0–1.5 km apart flying northward over Green River near what is now SLWMA.

Falconidae

Merlin (*Falco columbarius*). The species was seen in May and September 1937 (Twomey 1942) and September 1974 (Behle 1974). In an area including part of western Uintah County, two were sighted 29 December in 1954 (Crittenden et al. 1955) and 1955 (Killpack et al. 1956). I observed one flying over desert habitat in the vicinity of site 10 (Figs. 1–2). The species was more common in 1937 (Twomey 1942).

Peregrine Falcon (*Falco peregrinus*). Apparently less common (Fig. 2) than in 1937 (Twomey 1942). G. L. Richards observed a pair at what is now SLWMA in 1961 (Porter and White 1973), where Twomey (1942) saw the species. One was observed on three occasions in early May 1975 400 m north of Ignatio Stage Stop at T10S, R24E, Sec. 2 (Behle 1981). At ONWR, Peregrine Falcons were observed eating a Green-winged Teal 6 April 1981 (M. Lange, pers. comm.) and Red-winged Blackbirds 24 March 1982 (M. Lange and T. Tornow, pers. comm.). I saw an immature at 39°59′N, 109°31′W when the Desert Cottontail population in Uintah County was dense (unpubl. data). The bird flew away with a Desert Cottontail hanging from its talons. After flying about 30 m, the falcon alighted and allowed me to approach within 40 m of it. After remaining at one spot for about 7 min, it took off again. Peregrine Falcons seldom prey on mammals, although remains of hares, squirrels, and field mice have been seen near their nests (Bent 1961). A Peregrine Falcon seen by E. C. Peck and J. Gaskill in montane habitat 400 m southeast of Pine Spring, Uintah County 10 July 1966 was carrying a small jackrabbit (Behle 1981).

Galliformes

Phasianidae

Chukar (*Alectoris chukar*). Behle and Perry (1975b) and Behle (1981) noted that it is a common permanent resident in the oil shale area of Uintah County and northeastern Utah, respectively. However, the only records reported by Behle (1981) indicating that it occurred in what is possibly the desert region of Uintah County were of a flock of 20 and the collection of one specimen along Hill Creek 32–37 km south of Ouray 23 July 1966. Few observations of the species have been made in lowlands since. In Dinosaur National Monument, E. G. Goick saw 35 Chukars 25 January 1962 and the species in February 1965; J. W. Todd observed 2 birds 28 April 1963; S. Chalkley observed it 16 June 1975; D. C. Thompson sighted 3 birds 24 July 1963 and the species 1 October 1963 (D. Chure, in litt.).

From 1952 to 1966, 3005 Chukars were released at three sites, including Bitter Creek (Olsen 1973). They extended their range for several years and then declined in abundance (Olsen 1973). From 1977 to 1982, I observed none until shortly after many were stocked along Bitter Creek in 1981 by the Utah Department of Natural Resources, Division of Wildlife Resources. Three groups comprising about 70 tame individuals were observed near Bitter Creek between 5 and 12 km south of its confluence with White River (Figs. 1–2).

Sage Grouse (*Centrocercus urophasianus*). Three of the four leks that Olsen (1973) observed were apparently at least partially in desert habitat. Twomey (1942) saw the species only in mountains. L. Caterling (D. Chure, in litt.) observed two adults and four chicks one-third grown at or near the D. Chew Ranch south of southwestern Dinosaur National Monument (Fig. 1) 17 July 1965. I observed several birds along Road I in a greasewood stand near Willow Creek (Figs. 1–2). In 1982, personnel with the Utah Department of Natural Resources, Division of Wildlife Resources, located one lek on Deadman Bench east of Red Wash and another on East Bench southeast of Ouray (S. Madsen, pers. comm.). Two active leks possibly occurring in the desert region of Uintah County exist in Twelve-mile Wash north of U.S. Highway 40 and close to a seismological station near Asphalt Ridge (D. Zalunardo, pers. comm.).

California Quail (*Callipepla californica*). Introduced into the Uinta Basin about 1914 (Twomey 1942) and considered by Behle and Perry (1975a) and Hayward et al. (1976) to be well established in northern Utah. It was common in 1937 (Twomey 1942). A specimen was collected approximately 1.5 km south of Fort Duchesne 19 June 1966 (Behle 1981). I observed it only three times, twice along roads near agricultural land in Ashley Valley (at the intersection of 1500 North and 1500 East and on 500 East at about 1000 South) and once 50 m southeast of the Green River bridge at Ouray (Figs. 1–2). Twomey (1942) remarked that severe winters with heavy snowfall are detrimental to the quail. Perhaps, they were more common in 1937 than at present in Uintah County because of several years of mild or moderate winters prior to 1937.

Gruiformes

Rallidae

Virginia Rail (*Rallus limicola*). A. C. Lloyd (Twomey 1942) regarded it as common at what is now SLWMA in 1934 and 1935 and collected a juvenile male there on 9 August 1934. Twomey (1942) saw individuals along the west border of Ashley Creek marshes (SLWMA) in July and the last week of September 1937 and collected four. Only one sighting in what was possibly Uintah County has been recorded since 1937 (Killpack 1957). Using electronic recordings of the vocalizations of Virginia Rails, a member of Utah Field Ornithologists attracted two within view at ONWR 15 or 16 May 1982 when M. Lange heard many (M. Lange, pers. comm., Leppert 1982). The species was observed at PWA 19 May 1982 (S. Madsen, pers. comm.).

Sora (*Porzana carolina*). Uncommon in 1937 (Twomey 1942) and only one has been reported in published works since (Behle 1981). Utah Field Ornithologists sighted three 15–16 May 1982 at ONWR (Leppert 1982), where several nests were found in 1981 and 1982 (T. Tornow, pers. comm.). In spring 1982, a dead bird was found at ONWR, where it is preserved (M. Lange, pers. comm.). I heard the Sora at ONWR and on several occasions at a small marsh at site 4 (Figs. 1–2).

Common Moorhen (*Gallinula chloropus*). One observed at ONWR 24 May 1967 by E. C. Peck and associates (Behle 1981), 10–11 May 1977 by ONWR personnel (Behle 1981), in 1981 by T. Tornow (pers. comm.), and 1 May 1982 by D. Chure, M. Lange, L. Ferris, and N. Howk (M. Lange, pers. comm.).

Gruidae

Sandhill Crane (*Grus canadensis*). J. Metz saw one at SLWMA unusually early 20 February in 1981, and I observed a flock over site 4 3 June 1982, long after most members of the species had left Uintah County (Figs. 1–2).

Whooping Crane (*Grus americana*). As many as four birds were seen at ONWR or SLWMA until 6 October in 1976 and "all summer" in 1977 (Kingery 1976, Behle 1981). I observed one 11 October 1978 flying among a flock of about 70 south-bound Sandhill Cranes above the confluence of Bitter Creek and White River (Figs. 1–2). On 15 February 1981, J. Metz, an associate of the author, and C. Metz observed one at SLWMA (Kingery 1981b, Fig. 2) before the major migratory flock of Sandhill Cranes arrived in early April. At ONWR, one was seen by M. Lange on 5 October 1982 and by M. Lange, R. Clemens, and others 6 October 1982 (M. Lange, pers. comm.). H. G. Troester and M. Lange (pers. comm.) sighted an immature with an attached radio transmitter there 9 October 1982. At or near SLWMA, personnel of the Utah Department of Natural Resources, Division of Wildlife Resources, saw single individuals in 1981 and 1982, and D. L. Shirley and G. M. Webb sighted one adult and one immature in a flock of approximately 400 Sandhill Cranes 13 April 1983 (White et al. 1983).

Charadriidae

Black-bellied Plover (*Pluvialis squatarola*). Hayward (1966) stated that it is a "consistent and fairly common" migrant at Pelican Lake where he saw as many as 30 birds. Four specimens in the Brigham Young University avian collection were taken at Pelican Lake 13 May 1961, 18 May 1963, 2 June 1964, and 23 September 1961 (Hayward 1966, 1967). The species has not been reported since 1964. J. Metz and I saw a flock near the east shore of Pelican Lake and I saw one on the west side of the diked marsh at the northwest end of Pelican Lake (Figs. 1–2). Utah Field Ornithologists observed 2 at Pelican Lake 15–16 May 1982 (Leppert 1982).

Lesser Golden Plover (*Pluvialis dominica*). Twomey (1942) saw a flock of 46 in a plowed field south of Jensen 2 May 1937 and over what is now SLWMA 6 May 1937. One female was collected from a flock at Pelican Lake by Hayward (1966, 1967) 23 September 1961. C. Vigos, a consultant to Tosco Corporation, reported it 29–30 April 1976, and I observed it at Pelican Lake 27 April 1981 (Fig. 2).

Snowy Plover (*Charadrius alexandrinus*). Hayward (1967) observed a small flock at Pelican Lake 18 May 1963 and S. Hedges, R. Sorenson, and E. Sorenson saw four near Randlett (presumably at or near Pelican Lake) 2 May 1981 (Kingery 1981c). Utah Field Ornithologists saw two at Pelican Lake 15 or 16 May 1982 (Leppert 1982).

Semipalmated Plover (*Charadrius semipalmatus*). During "early May and September" of 1937, Twomey (1942) frequently observed two to five along sand bars of Green River and at the confluence of Green and White Rivers. Behle (1981) did not see it. The Brigham Young University avian collection includes two specimens collected at Pelican Lake 23 September 1961 and 29 September 1962 (Hayward 1967). Utah Field Ornithologists reported seeing two at Pelican Lake 15–16 May 1982 (Leppert 1982).

Killdeer (*Charadrius vociferus*). I did not observe it between 16 December and 24 February (Fig. 2) but in an area including western Uintah County, it was seen in late December 1952 and 1954–1958 (Crittenden 1953, 1955, Killpack 1957, 1958, 1959, Killpack et al. 1956).

Mountain Plover (*Charadrius montanus*). B. H. Green and A. R. Johnson saw it at Kennedy Basin (40°05′N, 109°17′W) 18 km northwest of Bonanza 9 May–20 June 1979 and also east of Bonanza (White et al. 1983).

Recurvirostridae

The **Black-necked Stilt** (*Himantopus mexicanus*) and **American Avocet** (*Recurvirostra americana*) have become more numerous (Fig. 2) in Uintah County since 1937 (Twomey 1942) due to the establishment of Pelican Lake and the marshes and ponds at ONWR and PWA.

Scolopacidae

Greater Yellowlegs (*Tringa melanoleuca*). Considered by Behle (1981) to be common migrants in northeastern Utah. Based on my observations of them at Pelican Lake, Woods Bottom of ONWR, and SLWMA (Fig. 2), they are uncommon. Since 1937 (Twomey 1942), they have also been observed in Uintah County in April, 15 May, and 22 July to 4 September during 1966, 1967, and 1980 (Anonymous 1977, Hayward 1967, Behle 1981, D. Chure, in litt.). At ONWR, 12 were observed 22–24 June 1981 (T. Tornow, pers. comm.), when the species is known to breed in Canada and Alaska (Bent 1962c), so the members of the flock were apparently nonbreeding summer residents.

Lesser Yellowlegs (*Tringa flavipes*). Evidently not as common now (Fig. 2) as in 1937 (Twomey 1942). Other sightings in Uintah County were made 20 July–23 September 1937, 1961, and 1966 (Hayward 1967, Behle 1981).

Solitary Sandpiper (*Tringa solitaria*). A. C. Lloyd (Twomey 1942) observed four or five almost every day of his study at what is now

SLWMA in 1934 and 1935. Twomey (1942) stated that in 1937 at least two pairs remained at the Ashley Creek marshes, where he presumed that they nested. A specimen housed at Brigham Young University was collected near Jensen 22 July 1937 (Hayward 1967). C. Vigos, a consultant to Tosco Corporation, saw it in the desert region of Uintah County 29 April 1976 (Fig. 2). I observed two at SLWMA and one at Pelican Lake (Fig. 2).

Willet (*Catoptrophorus semipalmatus*). Since 1937 (Twomey 1942), it has been observed 5 May–2 August 1966, 1967, 1977, and 1982 (Behle 1981, Leppert 1982). I observed young at Pelican Lake 23 June 1981. The creation of ponds and reservoirs in Uintah County in recent years accounts for the fact that it is now a common summer resident (Fig. 2).

Whimbrel (*Numenius phaeopus*). Seen by M. Webb in the Randlett area (presumably at or near Pelican Lake) in spring 1981 (Kingery 1981c). At the north end of the marsh situated at the northwest end of Pelican Lake, I observed one 21 May 1982 (Fig. 2).

Long-billed Curlew (*Numenius americanus*). Only four sightings of it in Uintah County have been published (Twomey 1942, Behle 1981). From 1979 to 1981 it was seen from April to August east of Green River at a water pump house approximately 4 km north of Woods Bottom Pond in ONWR, where it was believed to nest (T. Tornow, pers. comm.). At Wyasket Bottom of ONWR, M. Lange (pers. comm.) observed birds throughout their breeding season. T. Tornow (pers. comm.) saw young in 1979, and L. Littleton observed young several years earlier (T. Tornow, pers. comm.). H. L. Vickers and G. Limb, associates of the author, saw one approximately 6.5 km west of Bonanza on the Ouray-Bonanza road (T9S, R24E, Sec. 20) far from water 14 April 1982 (Fig. 2). Utah Field Ornithologists sighted eight at Pelican Lake 15–16 May 1982 (Leppert 1982).

Hudsonian Godwit (*Limosa haemastica*). Observed by birders R. Sorenson and E. Sorenson at a pond about 1 km west of Pelican Lake 2 May 1981, when seven were seen, and 5 May 1981, when two were observed (Kingery 1981c, M. L. Perry, pers. comm.). Those sightings constituted the second record of the species in Utah (Scott 1968). Hudsonian Godwits were seen by M. Webb and others in the Pelican Lake area 15 May 1982, when a male accompanying a flock of 60 Marbled Godwits was collected (the third record for Utah—Kingery 1982, Leppert 1982, White et al. 1983).

Marbled Godwit (*Limosa fedoa*). Nests in Canada and the northern plains of the U.S. in late May and in June (Bent 1962b), so birds that Hayward (1967) observed flying over Pelican Lake 2 June and those that A. C. Lloyd (Twomey 1942) saw during the first week of June were unusually late migrants. The abundance of the species in Uintah County has decreased since 1937 (Twomey 1942, Fig. 2).

Sanderling (*Calidris alba*). Apparently not as common (Fig. 2) as in 1935 and 1937 (Twomey 1942). Eight were collected on four occasions between 13 May 1961 and 12 May 1970 at Pelican Lake (Hayward 1967, Hayward et al. 1976), where my observations were made (Fig. 2).

Western Sandpiper (*Calidris mauri*). Considered by Hayward et al. (1976) to be an abundant migrant in Utah. Twomey (1942, 1944) saw hundreds during the first two weeks of May and in September 1937. Since then, only four published records have been made in Uintah County. Specimens were collected between 22 July 1961 and 13 May 1966 (Hayward 1967). I observed two on mud flats east and across Utah Highway 88 from Pelican Lake (Figs. 1–2). Utah Field Ornithologists observed one at Pelican Lake 15 or 16 May 1982 (Leppert 1982).

Least Sandpiper (*Calidris minutilla*). Regarded by Hayward et al. (1976) as an abundant migrant in Utah. However, records in Uintah County since 1937 (Twomey 1942) are few. At Pelican Lake, four sightings or collections were made 22 July 1961–19 September 1966 (Hayward 1967, Behle 1981). C. Vigos reported it 30 April–14 May 1976 (Fig. 2). Utah Field Ornithologists sighted one at Pelican Lake 15 or 16 May 1982 (Leppert 1982).

Baird's Sandpiper (*Calidris bairdii*). At Pelican Lake, two were collected 23 September 1961 (Hayward 1967) and one on both 19 August 1961 and 20 March 1967 (Behle 1981). No records in Uintah County have been made since. I observed three individuals on the east shore of the diked marsh at the northwest end of Pelican Lake (Figs. 1–2). The incidence of it has declined since 1937 (Twomey 1942), perhaps due to the human invasion and disturbance of its winter range in Argentina and Chile (Bent 1962a).

Dunlin (*Calidris alpina*). A. C. Lloyd (Twomey 1942) saw one in a flock of Least Sandpipers 1 May 1935, and Hayward (1967) observed several small flocks at Pelican Lake 15 May 1966. R. Sorenson and E. Sorenson saw Dunlins at Randlett (presumably in the Pelican Lake area) 2 May 1981 (Kingery 1981c). One was observed at the dry bed of the west pond of ONWR 8 November 1981 by B. Clemens, D. Chure, L. Ferris, and M. Lange (D. Chure, pers. comm.).

Long-billed Dowitcher (*Limnodromus scolopaceus*). Considered by Hayward et al. (1976) to be an abundant migrant. Based on both Twomey's (1942) study and mine (Fig. 2), it is an uncommon migrant in Uintah County, where it has been seen as early as 2 April (S. Madsen, pers. comm.) and as late as 10 November (Fig. 2).

Common Snipe (*Gallinago gallinago*). Considered to be common permanent resident in Utah (Behle and Perry 1975a, Hayward et al. 1976, Behle 1981). Based on Twomey's (1942) observations and mine (Fig. 2), it is uncommon in Uintah County. Most sightings there have been made April–June (Behle 1981, D. Chure and L. Ferris, pers. comm., Fig. 2); in an area including western Uintah County, from one to five birds were seen in late December of 1953–1958 (Crittenden et al. 1955, Killpack 1957, 1958, 1959, Killpack et al. 1954, 1956).

Wilson's Phalarope (*Phalaropus tricolor*). Although the species is less frequent during migration now (Fig. 2) than in 1937 (Twomey 1942), some are presently summer residents in Uintah County (Fig. 2), evidently due to the increased marsh area available there compared with 1937 when no summer residents occurred (Twomey 1942).

Red-necked Phalarope (*Phalaropus lobatus*). Regarded by Hayward et al. (1976) as an abundant migrant. C. L. Hayward and H. H. Frost (Hayward et al. 1976) observed thousands at Pelican Lake 15 May 1970. D. Zalunardo (pers. comm.) considers it an uncommon spring migrant at PWA. M. Lange (pers. comm.), a former employee at ONWR, did not see it there. I did not see the species in Uintah County, but M. Webb (Kingery 1981d) observed 400–500 birds at Duchesne, Duchesne County 9 May 1981 and Utah Field Ornithologists saw 50 in Myton, Duchesne County, 15 or 16 May 1982 (Leppert 1982).

Laridae

All species of Laridae that I observed more than once in Uintah County were evidently more abundant in this study (Fig. 2) than they were in 1937 (Twomey 1942), probably due to the creation of Pelican Lake and associated ponds and Woods Bottom Pond at ONWR.

Franklin's Gull (*Larus pipixcan*). Apparently more common now (Fig. 2) than in 1937 (Twomey 1942) but less prevalent now than 1961–1970 (Hayward 1967, Hayward et al. 1976, Behle 1981). Behle (1981) noted that it is a common summer resident in northeastern Utah. Based on this study, it is an uncommon migrant in Uintah County (Fig. 2).

Bonaparte's Gull (*Larus philadelphia*). Several were seen with a flock of Franklin's Gulls at Pelican Lake 15 May and 3 June 1970 (Hayward et al. 1976). The carcass of a subadult was found on the north shore of Pelican Lake 27 May 1977 (Behle 1981). At Fort Duchesne, 14 were seen by R. Sorenson and E. Sorenson 2 May 1981 (Kingery 1981c). I observed one adult and 8 immatures at the pond 1 km west of Pelican Lake and several immatures flying over Pelican Lake (Figs. 1–2). Utah Field Ornithologists sighted 4 birds in the Pelican Lake area 15–16 May 1982 (Leppert 1982).

Ring-billed Gull (*Larus delawarensis*). Considered by Behle and Perry (1975a) to be common winter visitants in northern Utah and to occur in the state 1 August–15 May. Behle (1981) noted that they probably do not nest in northeastern Utah. In Colorado the species is a migrant and nonbreeding resident (Bailey and Niedrach 1965).

Two or three were seen by Twomey (1942) along Green River throughout the summer of 1937, but they demonstrated no evidence of nesting (Twomey 1942). However, some ranchers owning property along Green River who were "careful bird observers" told Twomey (1942) "that during past years, a pair or two of the gulls nested on the large sand bars of Green River, between Jensen and the mouth of Green River Gorge" (probably Split Mountain). During this study, a flock of Ring-billed Gulls occurred at Pelican Lake and Woods Bottom Pond in ONWR throughout most of the year (Figs. 1–2). In 1981, several appeared to be nesting on an islet near the east end of Pelican Lake close to Utah Highway 88 (Figs. 1–2). I observed immature birds in that area in August 1981.

California Gull (*Larus californicus*). Twomey (1942) reported seeing one on Green River below Jensen 10 May 1937, and A. C. Lloyd (Twomey 1942) saw a flock of 50 at what is now SLWMA in mid-May 1935. Observed during 18–22 March, from 27 May or earlier that month to 4 June, and 22–27 July 1948, 1966, 1967, 1977, and unspecified years (Hayward 1967, Behle 1981). Flocks of gulls reside at Pelican Lake and at Woods Bottom Pond in ONWR, but I have observed no California Gulls in those flocks.

Herring Gull (*Larus argentatus*). Behle and others (Behle 1981) saw one at Pelican Lake 27 May 1977. I observed a large gull on Pelican Lake that I believe was a Herring Gull (Fig. 2).

Common Tern (*Sterna hirundo*). Utah Field Ornithologists reported three in the Pelican Lake area 15 May 1982 (Kingery 1982, Leppert 1982), but I have seen only Forster's Tern (*Sterna forsteri*) there.

Black Tern (*Chlidonias niger*). Hayward (1967) noted that it is a common summer resident at Pelican Lake in May, June, and July. It is apparently more prevalent now (Fig. 2) than in 1937 (Twomey 1942) but is uncommon. At ONWR, T. Tornow (pers. comm.) saw nests during 1979–1982, particularly at Leota Bottom in spring 1982 and M. Lange (pers. comm.) observed several nests in 1982.

Columbiformes

Columbidae

Band-tailed Pigeon (*Columba fasciata*). Observed on agricultural land south of La-Point (el. 1370 m) 19 May 1970 and in desert shrub habitat on Walker Hollow Road (el. 1830 m), which is south and southeast of Jensen, as close 13 km to that town, 30 April 1971 (Pederson and Nish 1975). D. Zalunardo (pers. comm.) sighted one in Vernal 23 October 1980 and M. Lange (pers. comm.) saw one during spring 1981.

Cuculiformes

Cuculidae

Yellow-billed Cuckoo (*Coccyzus americanus*). I closely observed and heard one in the Green River floodplain about 500 m southwest of the Green River bridge at Ouray in 1981 (Figs. 1–2). Also in 1981 and 1982, it was seen at ONWR by M. Lange (pers. comm.). The 1981 sightings constitute the first records of the species in northeastern Utah. Personnel of the Utah Department of Natural Resources, Division of Wildlife Resources, collected a carcass from the Maeser area northwest of Vernal in 1982 (J. S. Cranney, pers. comm.).

Strigiformes

Tytonidae

Common Barn-Owl (*Tyto alba*). Only two sightings of live birds have been recorded in northeastern Utah (Twomey 1942). Only one of them definitely occurred in the desert region of Uintah County, an individual seen by D. Stewart near Jensen in 1936 (Twomey 1942). One carcass that is now a part of the museum collection of Dinosaur National Monument, Utah, was collected at Jensen 29 November 1982 (D. Chure and L. Ferris, pers. comm.).

Strigidae

Western Screech-Owl (*Otus kennicottii*). Regarded as a common permanent resident in Utah (Behle and Perry 1975a, Hayward et al. 1976) but as uncommon in northeastern Utah (Behle 1981, Behle and Perry 1975b). A. C. Lloyd collected a female and three offspring she was feeding in dense willows at the confluence of Ashley Creek and Green River sometime between 25 and 30 July 1935 (Twomey 1942). Hayward (1967) observed the species near Jensen 18 May 1958. A nest found by M. Horton along upper Ashley Creek (Behle 1981) probably occurred in montane habitat. Ranger Sneddon and R. G.

Beidleman (Beidleman, in litt.) observed a small owl presumed to be a Western Screech-Owl in a box elder tree at the headquarters of Dinosaur National Monument 19 November 1946. On 22 May 1981, approximatey 750 m northwest of MFB, I was startled by a small owl, perhaps a Western Screech-Owl, which flew from a tree about 4 m behind me (Fig. 2).

Great Horned Owl (*Bubo virginianus*). Twomey (1942) did not observe it in Uintah County, apparently because it had been hunted extensively by "ranchers, farmers, and sportsmen." It is now common (Fig. 2).

Northern Pygmy-Owl (*Glaucidium gnoma*). Sighted in Dinosaur National Monument at Split Mountain Campground by J. Halfpenny 19 November 1982 and in cottonwood trees adjacent to a cave at the head of Red Rock Nature Trail, Split Mountain Campground, by D. Chure and L. Ferris (pers. comm.) 21 and 25 November 1982. One was also sighted at Dinosaur National Monument 26 December 1982 (D. Chure and L. Ferris, pers. comm.).

Northern Saw-whet Owl (*Aegolius acadicus*). Collected along a valley stream in Vernal 29 December 1957 (Hayward 1967). A nest containing three young was found by M. Horton 16 km east of Ouray in May 1967 (Behle and Perry 1975b, Behle 1981). H. G. Troester and M. Lange (pers. comm.) observed and photographed one individual at ONWR 3 February 1981.

Caprimulgiformes

Caprimulgidae

Common Poorwill (*Phalaenoptilus nuttalli*). Hayward (1967) stated that it is common in desert shrub and pinyon-juniper communities throughout the upper Colorado River basin but provided no sighting records. It is largely a montane species in northeastern Utah (Behle 1981). There is only one published record in the desert region of Uintah County, a male collected by A. C. Lloyd (Twomey 1942) 3 km south of Jensen 19 August 1935. One was sighted along the diked road in SLWMA about 800 m beyond the entrance sign by D. Chure and L. Ferris (pers. comm.) 6 September 1981; one was found dead near Pelican Lake 6 October 1982 by M. Lange (pers. comm.); Utah Field Ornithologists heard one at Split Mountain Campground, Dinosaur National Monument, 15 May 1982 (Leppert 1982).

Apodiformes

Trochilidae

Black-chinned Hummingbird (*Archilochus alexandri*). There are only five published records of it in the desert region of Uintah County (Twomey 1942, Hayward 1967). It is more commonly seen now than it was in 1937 (Twomey 1942), possibly due to more feeders around homes at the present time. In Dinosaur National Monument, one was observed at Dinosaur Quarry Residential Area by W. E. Welch 29 April 1965 and by W. G. Truesdell 12 June 1973 and at Prophecy in Stone, approximately 1 km southeast of Dinosaur Quarry Visitor Center, by N. Howk 22 June 1980 (D. Chure, in litt.). One male remained all summer at a feeder behind the house of D. Chure and L. Ferris along Utah Highway 149 (Road B, Fig. 1). By late July, the Black-chinned Hummingbird, as well as the other two species of hummingbirds in Uintah County, have begun leaving their montane nesting areas and appear in valleys, where they may remain until September (Fig. 2).

Broad-tailed Hummingbird (*Selasphorus platycercus*). Much more prevalent in the desert region of Uintah County during migration than during its nesting season (Twomey 1942, Leppert 1982, Beidleman, in litt., Fig. 2). Hayward (1967) supposedly found it nesting in a small crevice of a cliff "near the junction of White and Green Rivers, Duchesne County, Utah (elevation 6500 ft.)" 22 June 1954, where a female bird was seen feeding young. However, the confluence of White and Green rivers is in Uintah County at an elevation of about 1430 m (4700 ft). I observed a male in a cottonwood grove along the White River approximately 800 m northwest of MFB 2 June 1981 that may have been a breeding summer resident (Fig. 2).

Rufous Hummingbird (*Selasphorus rufus*). From 20 July to 11 August 1934, A. C. Lloyd (Twomey 1942) found at least three or four birds in each patch of fireweed (*Chamaenerion angustifolium*) that he examined. Lloyd saw only two individuals in 1935 and Twomey saw none in 1937 (Twomey 1942). In this study, it was commonly seen at site 4 and 800 m south of Naples, where J. Metz reportedly saw it 13 and 16 May 1981 (Figs. 1–2). One male was seen at a feeder in Logan, Cache County, 4–6 May 1982 by K. L. Dixon, who stated that the only other spring record in Utah occurred in 1962 (Kingery 1982).

Coraciiformes

Alcedinidae

Belted Kingfisher (*Ceryle alcyon*). Twomey (1942) observed the species three times. One was seen along Green River at ONWR during 18–22 March 1966 (Behle 1981), at "Leland" (presumably eastern Leland Bench) 13 April 1901 (Tullsen 1908), Sheppard Bottom of ONWR 1 May 1982, and Woods Bottom of ONWR in August 1981 (D. Chure, pers. comm.). D. Chure (pers. comm.) collected the carcass of a male at the junction of Utah Highway 149 and Brush Creek (Road B, Fig. 1) 7 May 1982. Two were sighted in the Jensen area 26 December 1982 (D. Chure and L. Ferris, pers. comm.). In an area including a part of western Uintah County, the species was seen 27 December 1956 and 29 December 1958 (Killpack 1957, 1959). I observed it approximately 700 m north of Ouray on the west side of Green River, near site 4, in flight near White River about 800 m northwest of MFB, and close to a stream about 1 km north of Pelican Lake (Figs. 1–2).

Piciformes

Picidae

Yellow-bellied Sapsucker (*Sphyrapicus varius*). Considered by Behle (1981) to be a common permanent resident in northeastern Utah that breeds from lowland riparian floodplains to aspen-pine forests. D. Gale (Bent 1964c) noted that in Colorado, it nests only in quaking aspens, usually at an elevation of 2440–2745 m. It has not been seen in the desert region of Uintah County during its breeding season in June (Bent 1964c) except on or about the federal oil shale tracts U-a and U-b in June 1975 (Anonymous 1977). The Yellow-bellied Sapsucker is apparently less common now (Fig. 2) than it was in 1937 (Twomey 1942). I observed it 200 m south of MFB (40°02′N, 109°27′W), about 1.7 km southwest of MFB (40°01′N, 109°28′W), and at ONWR (Figs. 1–2).

Downy Woodpecker (*Picoides pubescens*). Apparently less prevalent in the desert region of Uintah County now (Fig. 2) than in 1937 (Twomey 1942). No evidence was presented by Hayward (1967) to substantiate his claim that it is less commonly seen than the Hairy Woodpecker in valleys of the upper Colorado River basin during summer. The converse is true (Fig. 2). Hayward (1967) observed signs of nesting activity by the Downy Woodpecker on Green River floodplain near Ouray 17 May 1958. Nesting is apparently most common in June (Bent 1964b). My observations of the species in a cottonwood grove along the White River approximately 800 m northwest of MFB 2 and 23 June 1981 (Figs. 1–2) suggest that it may nest in White River lowlands.

Hairy Woodpecker (*Picoides villosus*). Since 1937 in the desert region of Uintah County, the only published record of it on a specific date regards a specimen collected at ONWR 31 July 1962 (Behle 1981). Despite reports (Hayward 1967, Hayward et al. 1976, Behle 1981) that the species nests in valley riparian sites, no specific sighting dates were given for lowland habitats during the Hairy Woodpecker's nesting period, which includes May and June (Bent 1964a). However, Beidleman (in litt.) observed a female in sagebrush at Split Mountain Campground, Dinosaur National Monument, 31 May 1957. One individual was seen at the headquarters of that monument by J. H. Lombard (Beidleman, in litt.) 1 September 1945. There was no evidence that the bird I saw along the White River 7 km southeast of Ouray 7 May 1982 (Figs. 1–2) was breeding. I also observed the species 350 m south of MFB and at ONWR (Fig. 2).

Passeriformes

Tyrannidae

Olive-sided Flycatcher (*Contopus borealis*). Not seen in the lowlands of northeastern Utah since 1937, when it occurred in "considerable numbers" along the main river valleys of the Uinta Basin 15 May–10 June and during September (Twomey 1942).

Western Wood-Pewee (*Contopus sordidulus*). Hayward (1967) stated that in the upper Colorado River basin, it is the most common small flycatcher inhabiting floodplain woodlands, where it breeds. All sightings in the desert region of Uintah County have occurred in May, June, and August (Twomey 1942, Behle and Ghiselin 1958, Behle 1981, Beidleman, in litt., D. Chure, in litt., Fig. 2) except an observation by the author on the Green River floodplain 500 m southwest of the Green River bridge at Ouray 1 September (Figs. 1–2). Those I saw 700–900 m northwest of MFB 27 May, 16 June, and 23 June 1981 (site 9, Figs. 1–2) may have been nesting. It is apparently less common now (Fig. 2) than it was in 1937 (Twomey 1942).

Willow Flycatcher (*Empidonax traillii*). Apparently less common now (Fig. 2) than in 1937 (Twomey 1942). Since then, it has been collected at Brush Creek about 13 km northeast of Vernal 24 August 1949, ONWR 22 August 1962, and the C.C.C. Crossing of Hill Creek approximately 65 km south of Ouray (possibly in the desert region of Uintah County) 23 August 1962 (Behle and Ghiselin 1958, Behle 1981). I observed it about 800 m northwest of MFB, at SLWMA, Split Mountain Campground, Dinosaur National Monument, near the transition of desert scrub habitat with montane habitat, and south and east of Green River at ONWR (Figs. 1–2).

Hammond's Flycatcher (*Empidonax hammondii*). The only member of the species that has definitely been observed in the desert region of Uintah County was collected by Twomey (1942) approximately 3 km south of Jensen in a cottonwood floodplain of what is now SLWMA 9 August 1937. An Empidonax flycatcher that I observed 1 km northwest of MFB on 27 May 1981 had a dark breast and throat except for a narrow whitish band along their center. Its general color was slaty. The bird was observed for about 10 minutes and did not make a sound. Hammond's Flycatcher is comparatively silent (Bent 1963d). However, its throat was not obviously darker than its breast and its mandible was yellowish brown like that of the Dusky Flycatcher. The mandible of Hammond's Flycatcher is usually blackish brown (Bent 1963d).

Dusky Flycatcher (*Empidonax oberholseri*). Behle (1981) indicated that it is a common migrant in the willows and cottonwoods of lowlands in northeastern Utah but provided only two records in valley habitats besides Twomey's (1942) observations: the collection of a specimen in the Uncompahgre Ute Indian Reservation by W. Granger 17 May 1895 and a sighting along White River at the mouth of Asphalt Wash 24 May 1975 (Behle 1981). In 1937, it was uncommon (Twomey 1942) and I found it to be rare (Fig. 2). Approximately 900 m northwest of MFB, I observed what I believed to be Dusky Flycatchers 12 and 27 May 1981. Their throats were not dark; the center of their bellies was yellow. The lower mandible of one bird was carefully observed with binoculars and was discovered not to be pied. The birds uttered a two-syllabled note resembling that described for the species (Bent 1963e).

Gray Flycatcher (*Empidonax wrightii*). Hayward et al. (1976) affirmed that it was widespread and the most common of the Empidonax flycatchers in Utah. Hayward (1967) attested that it is "by far the most common summer resident of any of the small flycatchers" in the upper Colorado River basin, although no specimen has been collected in the desert region of northeastern Utah (Behle 1981). Twomey (1942) observed only two members of the species in the Uinta Basin but none in its desert region. R. G. Beidleman (in litt.) saw the Gray Flycatcher 10 August and earlier in the same summer at Split Mountain Campground, Dinosaur National Monument. C. M. White (pers. comm.) collected it in desert scrub habitat in Utah. In this study, line transects were walked in that habitat in all seasons from 1977 to 1981. No Gray Flycatcher was seen there. Perhaps, because Uintah County is so arid, the species summers there only in the upper desert zone near juniper woodlands.

I observed two Gray Flycatchers in riparian habitat 200–400 m south of MFB for approximately four hours 7 September 1977 and 1.5 hours on 8 September 1977. The birds did not have an eye ring, but the presence of the latter is variably distinct among Empidonax flycatchers depending on the species and its molting stage. (Compare the conspicuousness of the eye rings of the Yellow-bellied Flycatcher, Western Flycatcher, and

Willow Flycatcher in the work of Terres [1980:366–367]). The Gray Flycatcher is less common in the Uinta Basin than in Utah generally, based on both Twomey's (1942) work and mine (Fig. 2).

Western Flycatcher (*Empidonax difficilis*). Regarded by Behle and Perry (1975a) and Behle (1981) as a common summer resident in the canyons and mountains of Utah and northeastern Utah, respectively. However, Hayward et al. (1976) considered it to be a sparse breeder in Utah mountains. The only member of the species seen by Twomey (1942) in what was possibly the desert region of Uintah County was collected 16 km west of Vernal 28 May 1937. I observed a Western Flycatcher in cottonwoods 900 m northwest of MFB (Fig. 2).

Eastern Phoebe (*Sayornis phoebe*). One reported in riparian habitat on or about the federal oil shale tracts U-a and U-b in October 1976 (Anonymous 1977). On 1 May 1981, J. Metz and I observed an apparent hybrid between an Eastern Phoebe and a Say's Phoebe, although its characteristics fitted those of the former much more closely. It was observed in badlands habitat about 800 m southwest of MFB (40°02′N, 109°28′W) along an avian transect. The bird repeatedly alighted on and took flight from a 2.4-m marker that had been placed on the center line of the transect. We watched it for about 15 minutes from a distance as near as 15 m and then continued to walk the line transect to its termination. Thereafter, we began walking the center line of the transect in the opposite direction and again encountered the bird at the site where we had initially spotted it. We watched it for an additional 5 minutes. The flycatcher had a dark head and bill and a white throat. It lacked wingbars and bobbed its tail up and down. However, it possessed a faint washing of cinnamon on the belly. I refer to the bird as an Eastern Phoebe in Fig. 2 because its traits matched those of that species except for the slight rusty tint on its venter.

Say's Phoebe (*Sayornis saya*). Hayward (1967) stated that it prefers to occupy open desert sites. Bent (1963c) affirmed that Say's Phoebe is a bird of open country, sagebrush plains, badlands, dry, barren foothills, and the margins of deserts, where it forages over low vegetation, and added that it is not fond of water courses or woods. I walked avian transects in desert habitat, including badlands, over all seasons during four years and did not see the species there. I saw it only in or about riparian habitat at PWA, MFB, about 1 km southwest of MFB, along White River between the West Fork of Saddle Tree Draw and MFB (Route 15), and along Green River approximately 250 m below the Green River bridge at Dinosaur National Monument (Figs. 1–2). Say's Phoebe is less common (Fig. 2) than it was in 1937 (Twomey 1942).

Vermilion Flycatcher (*Pyrocephalus rubinus*). At the headquarters of ONWR, it was reported by M. Lange, R. Sjostrom, and H. G. Troester 4 October 1982 and by M. Lange 7 November 1982 (M. Lange and H. G. Troester pers. comm.). Those sightings are among the first in northern Utah.

Ash-throated Flycatcher (*Myiarchus cinerascens*). In the desert region of Uintah County, it is more prevalent during migration than summer. Nesting incidence apparently peaks in late June (Bent 1963b), when I saw it (23 June) in cottonwoods along White River 1 km northwest of MFB (Fig. 2).

Western Kingbird (*Tyrannus verticalis*). Twomey (1942) stated that it was "among the most characteristic birds" of the Green River floodplains in 1937. Although the species has extended its range during the last century (Bent 1963a), it is presently less abundant in Uintah County (Fig. 2) than it was in 1937 (Twomey 1942), possibly due to the loss of suitable habitat on its wintering grounds in western Central America (Bent 1963a). At "Leland" (presumably eastern Leland Bench), Tullsen (1908) saw the species 31 March as well as 7–9 April 1901, a month earlier than I did (Fig. 2).

Eastern Kingbird (*Tyrannus tyrannus*) Apparently less common in northeastern Utah (Twomey 1942, Behle 1981, Fig. 2) than in northern Utah in general (Behle and Perry 1975a). I observed it only in May and August (Fig. 2), but it has also been seen in June and July (Twomey 1942, Behle and Ghiselin 1958, Behle 1981).

Alaudidae

Horned Lark (*Eromphila alpestris*). Twomey (1942) believed that it arrived in the

Uinta Basin in April during snowmelt. However, it is a permanent resident there (Fig. 2) and is at least as abundant now (Fig. 2) as it was in 1937 (Twomey 1942).

Hirundinidae

Purple Martin (*Progne subis*). Twomey (1942) observed 30 about bird houses in Vernal during 1937. Argante (D. Chure, in litt.) saw it at Green River Campground, Dinosaur National Monument, 1 June 1973.

Tree Swallow (*Tachycineta bicolor*). Considered by Behle and Perry (1975a) to be a common summer resident in Utah, but Twomey (1942) did not observe it. W. G. Truesdell sighted 15–20 at Dinosaur Quarry Residential Area 24 April 1973, and Argante saw the species at Green River Campground, Dinosaur National Monument, 1 June 1973 (D. Chure, in litt.). C. Vigos, a consultant to Tosco Corporation, saw it in the desert region of Uintah County (Fig. 2). I observed Tree Swallows near Green River about 1 km south of Dinosaur Quarry Visitor Center, Dinosaur National Monument, and feeding over a marsh at ONWR (Figs. 1–2).

Violet-green Swallow (*Tachycineta thalassina*). In the desert region of Uintah County, it is evidently less plentiful now (Fig. 2) than in 1937 (Twomey 1942). It is most prevalent at montane canyon cliffs. At Dinosaur National Monument, it was sighted at least eight times from 15 May to August in 1942, 1956, 1957, 1973, and 1982 (Leppert 1982, Beidleman, in litt., D. Chure, in litt.). A specimen was collected about 6.5 km north of Green River 22 June 1947 (Behle 1981).

Northern Rough-winged Swallow (*Stelgidopteryx ruficollis*). Twomey (1942) spotted individual Northern Rough-winged Swallows in congregating flocks of Bank Swallows in August and September 1937. Twice I observed a small flock of Northern Rough-winged Swallows at SLWMA (Fig. 2). Utah Field Ornithologists saw one bird in a Vernal City park 15 May 1982 (Leppert 1982). It is less common now than in 1937 (Twomey 1942).

Bank Swallow (*Riparia riparis*). Apparently less common now (Fig. 2) in the desert region of Uintah County than in 1937 (Twomey 1942). Behle and colleagues (Behle 1981) saw it only twice in northeastern Utah and only once in the desert region of Uintah County—at Pelican Lake 27 May 1977 (Behle 1981). The American Museum of Natural History contains a specimen collected by W. Granger on the Uncompahgre Ute Indian Reservation 31 May 1895 (Behle 1981). I observed it near Green River 1 km south of Dinosaur Quarry Visitor Center, Dinosaur National Monument (Fig. 2). Utah Field Ornithologists observed 200 at ONWR and 12 at Pelican Lake 15–16 May 1982 (Leppert 1982).

Corvidae

American Crow (*Corvus brachyrhynchos*). Twomey (1942) noted that in 1937 it was numerous during migration along the Green River valley. He found six nests at what is now SLWMA. Hayward (1967) stated that in the Green River Basin Province, the American Crow occurs regularly in summer, where it nests in trees and willow thickets along streams. It occurs sparingly in western counties of Colorado (Bailey and Niedrach 1965). I saw it only in the winter of 1977–1978 (Fig. 2) on Road F approximately 10 km east of Ouray (Fig. 1). On Audubon Christmas counts in an area including part of western Uintah County, M. L. Killpack and associates observed 4 on 27 December 1951 (Killpack et al. 1952), 26 on 23 December 1952 (Crittenden et al. 1953), 3 on 31 December 1953 (Killpack et al. 1954), 2 on 29 December 1954 (Crittenden et al. 1955), 11 on 27 December 1956 (Killpack 1957), 38 on 31 December 1957 (Killpack 1958), and 368 on 29 December 1958 (Killpack 1959). However, most of those observations may have occurred in eastern Duchesné County, where I have frequently seen the species. At a nesting site about 11 km south of Whiterocks in what was probably the desert region of western Uintah County, M. L. Killpack (Richards and White 1963) banded 3 nestlings on 20 May 1953.

Common Raven (*Corvus sinuatus*). Behle (1981) provided no sighting or collection records of his own. In the desert region of Uintah County, it was seen by W. Granger in 1895 (Behle 1981), Twomey in 1937 (Twomey 1942), and Killpack and two associates in an area including part of western Uintah County 29 December 1955 (Killpack et al. 1956). D. B. Beard (Beidleman, in litt.) saw a few around the headquarters of Dinosaur National Monument at "various times," including 12 August 1942. Utah Field Ornithologists sighted five birds at Josie Morris Cabin, Dinosaur National Monument, and one bird at SLWMA 15–16 May 1982 (Leppert 1982). I observed it along Road F (Fig. 1) 5–15 km east of Ouray in desert scrub habitat near agricultural land 29 September 1978 and during the winter of 1977–1978 (Fig. 2). The Common Raven, like the American Crow, is less common in Uintah County (Fig. 2) than elsewhere in Utah (Behle and Perry 1975a, Hayward et al. 1976). I frequently observe both species in Duchesne County along U.S. Highway 40. Perhaps they are more common in Duchesne County because of its closer proximity to the relatively mesic valleys of central Utah.

Paridae

Black-capped Chickadee (*Parus atricapillus*). Common both in 1937 (Twomey 1942) and now (Fig. 2). At least nine sightings by others were made in the desert region of Uintah County from 19–22 March and 15 May to 26 August in 1949, 1950, 1966, 1967, 1974, 1981, and 1982 (Behle and Ghiselin 1958, Behle 1981, Leppert 1982, D. Chure, in litt.). I observed it during every month except January but saw it 31 December and 2 February and consider it a permanent resident (Fig. 2).

Mountain Chickadee (*Parus gambeli*). Few sightings have been made of it in the desert region of Uintah County. In an area including western Uintah County, six were seen 23 December 1952 (Crittenden et al. 1953). A specimen collected at the C.C.C. Crossing of Hill Creek approximately 65 km south of Ouray 23 August 1961 (Behle 1981) may have occurred in the desert region of Uintah County. Hayward (1967) stated that it was "rather common" in cottonwood groves along White River near Bonanza in late September 1966. It was observed near Josie Morris Cabin, Dinosaur National Monument by K. Truesdell 15 March 1974 and by W. G. Truesdell 29–30 March 1974 (D. Chure, in litt.). I observed one about 300 m southeast of the Green River bridge at Ouray (Figs. 1–2).

Sittidae

Red-breasted Nuthatch (*Sitta canadensis*). Observed at Josie Morris Cabin, Dinosaur National Monument, 15 May 1982 (Leppert 1982), in cottonwoods near Ouray 17 May 1958 (Hayward 1967), in cottonwood groves along White River 800 m northwest of MFB 21 May 1982 and 300 m south of MFB 9 September 1981 (site 9, Figs. 1–2), and near the confluence of Ashley Creek and Green River 30 September 1937 (Twomey 1942).

White-breasted Nuthatch (*Sitta carolinensis*). One was seen in an area including western Uintah County 31 December 1953 (Killpack et al. 1954). Another was collected from the Green River floodplain near Ouray 17 May 1958 and from White River south of Bonanza 19 September 1966 (Hayward 1967). Hayward (1967) noted that the species was common in cottonwood groves south of Bonanza in May 1958, when individuals appeared to be preparing to nest. C. Vigos, a consultant to Tosco Corporation, reported that she observed it 23 October 1976 (Fig. 2).

Troglodytidae

Canyon Wren (*Salpinctes mexicanus*). Since 1937 (Twomey 1942) all sightings or collections of it except one (Behle 1981) have been made in Dinosaur National Monument. It was seen there by Argante 1 June 1973 (D. Chure, in litt.), B. Ingber 9 July 1980 (D. Chure, in litt.), D. B. Beard in July and August (including 12 August) and 14 September 1942 (Beidleman, in litt.) and was heard there by J. H. Lombard 29 August 1945 (Beidleman, in litt.). At Split Mountain Campground, Dinosaur National Monument, it was heard 26 August 1981 (Fig. 2) and seen 15 or 16 May 1982 (Leppert 1982). Also at Dinosaur National Monument, I heard one on a rock face approximately 50 m high near a picnic area about 300 m below the Green River bridge 11 August 1981 (Fig. 2), and Utah Field Ornithologists saw seven at Josie Morris Cabin 15 or 16 May 1982 (Leppert 1982).

Bewick's Wren (*Thryomanes bewickii*). Observed at SLWMA and along Utah Highway 149 (Road B, Fig. 1) between Jensen and Dinosaur National Monument (Behle and Perry 1975a). Other sightings and collections of it may have occurred in juniper-pinyon habitat (Hayward 1967, Killpack and Hayward 1958), although the observation of two birds at Cub Creek near Josie Morris Cabin, Dinosaur National Monument, 15 May 1982 probably did not (Leppert 1982, D. Chure, pers. comm.).

Marsh Wren (*Cistothorus palustris*). More common (Fig. 2) than it was in 1937 (Twomey 1942) and most prevalent at site 3 (Fig. 1).

Muscicapidae

Golden-crowned Kinglet (*Regulus satrapa*). One sighted in riparian habitat near ONWR 1 May 1982 by M. Lange, D. Chure, L. Ferris, and N. Howk (M. Lange, pers. comm.).

Ruby-crowned Kinglet (*Regulus calendula*). Considered by Behle (1981) to be a common permanent resident in northeastern Utah but the only sighting records in valleys that he provided were those of Twomey (1942). It is less common now (Fig. 2) than in 1937, when Twomey (1942) saw flocks of 10–30 during migration. In the desert region of Uintah County, more than 11 other sightings were made 18 April–16 May and 7 October–10 November in 1945, 1951, 1956, 1957, 1975, 1976, and 1982 (Anonymous 1977, Leppert 1982, Beidleman, in litt., D. Chure, in litt.).

Blue-gray Gnatcatcher (*Polioptila caerulea*). A. C. Lloyd (Twomey 1942) collected one approximately 3 km south of Jensen 20 May 1935. The species, although uncommon, is more prevalent now (Fig. 2). Not many more than eight sightings were made 26 April–30 May and 25 July in 1956, 1957, 1965, 1974, 1975, and 1982 (Behle 1981, Leppert 1982, Beidleman, in litt., D. Chure, in litt.). In 1949 Weston (1964) reported that "the Uinta Valley near Vernal" was at the northern boundary of the Blue-gray Gnatcatcher's range. Its range shifted northward between 1937 and 1967. In 1967 it was reportedly a common summer resident in the Uinta Mountain Province (Hayward 1967).

Black-tailed Gnatcatcher (*Polioptila melanura*). One was reported by ornithologists with the White River Shale Project team in sagebrush-greasewood, riparian, and juniper habitats during April and August 1975 (Anonymous 1977). W. G. Truesdell (D. Chure, in litt.) reported sighting one in juniper habitat near Josie Morris Cabin, Dinosaur National Monument, 14 May 1974.

Mountain Bluebird (*Sialia currucoides*). Considered to be a common summer resident in Utah (Behle and Perry 1975), northeastern Utah (Behle 1981), and the oil shale region of Uintah County (Behle and Perry 1975b). It is a common permanent resident in the desert region of Uintah County (Fig. 2). Winter sightings include observations of 2–13 in an area including western Uintah County during late December 1951, 1952, and 1954–1956 (Crittenden et al. 1953, 1955, Killpack 1957, Killpack et al. 1952, 1956) and observations of one on Road N about 1 km north of Fort Duchesne 20 January 1982, near MFB 8 March 1979, and at site 8 on 14 March 1980 (Figs. 1–2).

The Mountain Bluebird is less common in lowlands than formerly due to disturbances by Starlings and House Sparrows (Hayward 1967, Hayward et al. 1976). During its presumed nesting season, I observed the species four times. In May 1982, J. M. Merino and J. Morehouse, associates of the author, found a nest south of White River near MFB (site 9, Figs. 1–2).

Townsend's Solitaire (*Myadestes townsendi*). Reported to be common in Utah (Behle and Perry 1975a) and northeastern Utah (Behle 1981) but is uncommon in the desert region of Uintah County (Twomey 1942, Fig. 2). In an area including western Uintah County, three individuals were observed 27 December in 1951 (Killpack et al. 1952) and 1956 (Killpack 1957). It was seen along White River at the mouth of Atchee Creek 25 May 1975 (Behle 1981) and collected about 5 km south of Bonanza 21 September 1966 (Hayward 1967). At Dinosaur National Monument, one was observed at Dinosaur Quarry Residential Area 13 February 1964 and at Cub Creek near Josie Morris Cabin 15 May 1982 (Leppert 1982, D. Chure, in litt.). C. Vigos observed it 29 October 1976 (Fig. 2). I observed one along White River in cottonwood groves both 400 m south and 800 m northwest of MFB and also at site 4 (Figs. 1–2).

Veery (*Catharus fuscescens*). One in the Royal Ontario Museum was collected at Jensen in July 1935 (Hayward et al. 1976). I saw one bird in a cottonwood grove approximately 300 m south of MFB 10 May 1978 (Fig. 2).

Swainson's Thrush (*Catharus ustulatus*). Regarded by Behle (1981) as a common summer resident showing altitudinal migration in northeastern Utah. Sightings of it in the desert region of Uintah County are few. A. C. Lloyd (Twomey 1942) collected one at what is now SLWMA 29 May 1935. At Dinosaur National Monument W. G. Truesdell (D. Chure, in litt.) sighted one at Dinosaur Quarry Residential Area 5 May 1973, and Utah Field Ornithologists saw one in Hog Canyon near Josie Morris Cabin (possibly in the desert region of Uintah County) 15 May 1982 (Leppert 1982, D. Chure, pers. comm.). Twice, I observed one along White River 800–900 m northwest of MFB (Figs. 1–2).

Hermit Thrush (*Catharus guttatus*). Evidently not as common (Fig. 2) as in 1937 (Twomey 1942). Specimens were collected 34 km north of Green River 24 May 1947 (Behle 1981) and along White River approximately 5 km south of Bonanza 21 September 1966 (Hayward 1967). The species was observed at the confluence of White River and Atchee Creek 25 May 1975 (Behle 1981) and at Cub Creek, Dinosaur National Monument, by N. Howk and B. Ingber 14 August 1981 (D. Chure, in litt.). I saw one in a cottonwood grove near White River about 800 m northwest of MFB (Figs. 1–2).

Mimidae

Gray Catbird (*Dumetella carolinensis*). Twomey (1942) reported that it was "numerous during the spring migration" in 1937 and that four pairs nested at the Ashley Creek marshes at what is now SLWMA. A. C. Lloyd (Twomey 1942) did not see it at what is now SLWMA in 1934 but indicated that it was common there in 1935. In the vicinity of the Ashley Creek marshes, a juvenile was collected in 1935 and seven adults in 1937 (Twomey 1942). Three were collected at two other sites: approximately 5 km south of Vernal 9 July 1949 and at Merkley Park in montane-riparian habitat 16 km north of Vernal 21 June 1949 (Behle and Ghiselin 1958). D. Chure and L. Ferris (pers. comm.) saw one 800 m within SLWMA 9 August 1981. I did not observe the species.

Northern Mockingbird (*Mimus polyglottus*). Sightings were made of one to four on several occasions 1927–1937 (Twomey 1942) and the species 9 June 1953 and 16 June 1954 (Killpack and Hayward 1958). I observed it in desert habitat near site 10 (Figs. 1–2). T. Tornow and M. Lange (pers. comm.) saw it at ONWR from spring to early summer in 1979–1982 and assumed that it nested there during those years. Young were seen around residences at ONWR in 1977 (T. Tornow pers. comm.).

Bendire's Thrasher (*Toxostoma bendirei*). A pair of birds feeding one of its young in proximity to Sage Thrashers was observed and photographed by A. R. Johnson and B. H. Green at Coyote Wash 17 km northeast of Bonanza 30 (or 31) May–4 June 1980 (Kingery 1980b, White et al. 1983). E. Sorenson and R. Sorenson (Kingery 1981d) saw two at Randlett 7 July 1981.

Motacillidae

Water Pipit (*Anthus spinoletta*). Seen by Twomey (1942) on mud flats of Ashley Creek and Green River at what is now SLWMA during 1–26 May and 20–29 September 1937. In an area including part of western Uintah County, M. L. Killpack and associates observed 27 on 29 December 1955 (Killpack et al. 1956), 2 on 27 December 1956 (Killpack 1957), and one on 29 December 1958 (Killpack 1959). J. Metz observed it at ONWR 2 April 1981 and C. Vigos reportedly saw it 29 April, 13 May, 23 October, and 5–6 November 1976 (Fig. 2).

Bombycillidae

Bohemian Waxwing (*Bombycilla garrulus*). Behle (1981) indicated that in northeastern Utah it is generally a common but erratic winter visitant. In an area including western Uintah County, 61 were observed 27 December 1956 (Killpack 1957) and 780 were seen 29 December 1958 (Killpack 1959). At site 4 (Fig. 1), I observed a flock in 1979 and 1980 (Fig. 2).

Laniidae

Northern Shrike (*Lanius excubitor*). Seen 18 March 1966 and 22 March 1967 (Behle

1981) and 31 December 1981 and 12 January 1982 (Fig. 2). In an area including part of western Uintah County, it was observed 27 December 1956 (four, Killpack 1957), 29 December 1958 (two, Killpack 1959), and 31 December 1957 (four, Killpack 1958).

Loggerhead Shrike (*Lanius ludovicianus*). Least common during winter. In an area including part of western Uintah County, it was seen during late December 1951–1956 (Crittenden et al. 1953, 1955, Killpack 1957, Killpack et al. 1952, 1954, 1956). I saw this common permanent resident during midwinter 28 January, as well as in other periods (Fig. 2).

Vireonidae

Gray Vireo (*Vireo vicinior*). Reported in Dinosaur National Monument at Josie Morris Cabin by J. C. Sinclear 18 May 1979 and along Cub Creek between the petroglyph site and Josie Morris Cabin by D. Chure and L. Ferris 5 July 1981 (D. Chure, in litt.).

Warbling Vireo (*Vireo gilvus*). Reported to be a common summer resident in the willows and cottonwoods of riparian floodplains as well as in mountains (Hayward 1967, Behle 1981). In the desert region of Uintah County it is an uncommon migrant (Twomey 1942, Fig. 2). One was collected along White River 8 km east of Bonanza 26 May 1974 and at ONWR 22 August 1962 (Behle 1981). In trees about Dinosaur Quarry Residential Area, Beidleman (in litt.) observed a pair for several days prior to and on 30 April 1956, and N. Howk sighted it 25 August and 11 September (with B. Ingber) 1981 and 22 May 1982 (D. Chure, in litt.). Utah Field Ornithologists saw 3 at Josie Morris Cabin, Dinosaur National Monument (possibly in the desert region of Uintah County), 15 May 1982. I observed 10 along White River 900 m northwest of MFB and the species 800 m northwest of MFB (site 9, Figs. 1–2).

Philadelphia Vireo (*Vireo philadelphicus*). I observed it in a tamarix bush near White River approximately 1.3 km southwest of MFB (40°01′N, 109°28′W) 25 September 1979 and in a cottonwood tree 450 m south of MFB (40°02′N, 109°27′W) 27 September 1979 (site 9, Figs. 1–2). It was reported at Salt Lake City, Salt Lake County, 15 September 1964 (Scott 1965), in 1966 (Scott 1969), and 22 September 1968 (Scott 1969). The first record of it in Nevada occurred 6 May 1981 when C. Lawson (Kingery 1981c) saw one at a bird bath in Las Vegas.

Red-eyed Vireo (*Vireo olivaceus*). Twomey (1942) heard it almost every day 29 May–9 June 1937 and observed it 20–28 September 1937 apparently at what is now SLWMA. He collected one about 6.5 km south of Jensen (Twomey 1942). Since 1937 the only report of the species in the desert region of Uintah County was on the federal oil shale tracts U-a and U-b in riparian habitat in June 1975 (Anonymous 1977). B. Webb (Kingery 1979b) heard and possibly observed one bird at Dinosaur National Monument 31 May 1979, but it probably occurred in Colorado.

Emberizidae

Tennessee Warbler (*Vermivora peregrina*). One was reported at Josie Morris Cabin, Dinosaur National Monument, by D. Chure, L. Ferris, M. Leppert, and J. Burns 15 May 1982 (Leppert 1982, D. Chure, pers. comm.).

Orange-crowned Warbler (*Vermivora celata*). At what is now SLWMA, Twomey (1942) saw four 10 May 1937 and a few 25 September 1937. One was collected 29 September 1937 from a small flock of five occurring in dense willows and cottonwoods on the Ashley Creek floodplain immediately south of the Ashley Creek marshes (Twomey 1942). In Dinosaur Quarry Residential Area L. M. King (D. Chure, in litt.) sighted it in shrubs 30 April 1975. Utah Field Ornithologists saw four at Josie Morris Cabin, Dinosaur National Monument, 15 May 1982 (Leppert 1982). I observed one both 250 and 500 m south of MFB and also at ONWR (Figs. 1–2).

Virginia's Warbler (*Vermivora virginiae*). Apparently less common (Fig. 2) than it was in 1937 (Twomey 1942). In Dinosaur National Monument, N. Howk (D. Chure, pers. comm.) sighted two along Cub Creek 14 August 1981, and J. C. Sinclear (D. Chure, in litt.) observed the species at a stream bed along Red Rock Nature Trail 16 May 1979 and in deciduous trees at Josie Morris Cabin 18 May 1979. At the latter site, Utah Field Ornithologists saw four 15 May 1982 (Leppert 1982). D. Chure and L. Ferris (pers. comm.) observed it in thickets along the road in SLWMA 6 August 1981. I saw it about

400 m south of MFB in tamarix bushes, 600 m northwest of MFB in cottonwoods, and along Brush Creek at site 1 (Figs. 1–2).

Yellow-rumped Warbler (*Dendroica coronata*). Although a common migrant in the desert region of Uintah County, it is less abundant now (Fig. 2) than in 1937 (Twomey 1942). Behle (1981) indicated that it is a migrant in desert scrub as well as lowland riparian and pinyon-juniper habitats, but I saw only one in desert scrub habitat during five years. Utah Field Ornithologists reportedly saw a member of the Myrtle subspecies at SLWMA 15 or 16 May 1982 (Leppert 1982).

Townsend's Warbler (*Dendroica townsendi*). I observed one in the upper canopy of a cottonwood tree near White River about 300 m south of MFB 11 September 1981 (site 9, Figs. 1–2). D. Chure, J. Burns, and M. Leppert sighted one at Josie Morris Cabin, Dinosaur National Monument, 15 May 1982 (Leppert 1982, D. Chure, pers. comm.).

American Redstart (*Setophaga ruticilla*). Twomey (1942) observed a pair 20 September 1937 in dense willows at what is now SLWMA, where a specimen was collected by A. C. Lloyd 20 August 1935. W. G. Truesdell (D. Chure, in litt.) observed it at Dinosaur Quarry Residential Area, Dinosaur National Monument, 19 September 1973. One was collected at the confluence of Atchee Creek and White River 25 May 1975 (Behle 1981) and observed in spring 1981 at ONWR (M. Lange, pers. comm.).

MacGillivray's Warbler (*Oporornis tolmiei*). Behle (1981) indicated that in northeastern Utah it is a common summer resident that may occur anywhere in the lowlands, including desert scrub vegetation, during migration. One was collected about 5 km south of Vernal 27 August 1949 (Behle and Ghiselin 1958). The migrant population of the species in the desert region of Uintah County has decreased considerably since 1937 (Twomey 1942, Fig. 2). In Dinosaur National Monument a male was seen in bushes behind the Dinosaur Quarry Apartments by J. Freilich 14 September 1978 and two were observed in box elder trees and underbrush at Cub Creek near Josie Morris Cabin by N. Howk 29 August 1981 (D. Chure, in litt.). I observed one in shrubbery along the diked road at SLWMA and in a cottonwood grove approximately 200 m south of MFB (Figs. 1–2).

Common Yellowthroat (*Geothlypis trichas*). Apparently less common now (Fig. 2) than it was in 1937 (Twomey 1942).

Wilson's Warbler (*Wilsonia pusilla*). Evidently less common now (Fig. 2) than in 1937 (Twomey 1942) in the desert region of Uintah County but, both in the 1930s (1934–1935 compared with 1937) and in recent years (1977–1980 compared with 1981), its abundance during migration has varied markedly among years (Twomey 1942, Fig. 2). In the desert region of Dinosaur National Monument, Wilson's Warbler was observed on 11 different days 15 May–7 June and 1 September–9 October in 1950, 1973, 1981, and 1982 (Leppert 1982, Beidleman, in litt., D. Chure, in litt.). Other sightings in the desert region of Uintah County were also made in May, June, September, and October in 1948 and 1974–1976 (Behle and Ghiselin 1958, Hayward 1967, Anonymous 1977, Behle 1981, Leppert 1982).

Yellow-breasted Chat (*Icteria virens*). In the desert region of Uintah County more than 16 sightings of it were made 15 May–24 August in 1949, 1966, 1973–1976, 1981, and 1982 (Behle and Ghiselin 1958, Anonymous 1977, Behle 1981, Leppert 1982, D. Chure, in litt.), but it seems to be less common now (Fig. 2) than it was in 1937 (Twomey 1942). It is more prevalent at Hill and Willow Creeks than at White and Green Rivers. Along White River it occurred only where the river bordered abruptly with thickets.

Western Tanager (*Piranga ludoviciana*). Behle (1981) noted that in northeastern Utah it occurs widely in lowland woods during migration. According to both Twomey's (1942) study and mine (Fig. 2), it is an uncommon migrant in the desert region of Uintah County. More than 10 other sightings of the Western Tanager were made there from 15 May or earlier that month to 31 May and during August, including 24 August 1895, 1957, 1975, 1976, 1979, and 1982 (Behle 1981, Leppert 1982, Beidleman, in litt., D. Chure, in litt.). Hayward (1967) remarked that spring migrants, usually in pairs, were seen in streamside woods in the Uinta Basin 2 June and 22 July, suggesting that perhaps some members nest in lowlands there. In Vernal, I saw a male 5 June 1982; near White River 700–850 m northwest of MFB, I observed several 2 June and one female 16 June 1981

(Figs. 1–2). However, the Western Tanager was not seen northwest of MFB 23 June and was not observed in any part of the desert region of Uintah County in July. Twomey (1942) observed fall migrants in scattered locations during the first two weeks of September 1937, but the latest that I saw the species was 11 August (Fig. 2).

Black-headed Grosbeak (*Pheucticus melanocephalus*). Reported to be rather common (Hayward 1967) or common (Behle 1981) in lowland riparian woodlands, mountains, and ornamental trees in parks or around homes. I never saw it in my yard. There has been a marked decline in its incidence in the desert region of Uintah County since 1937 (Twomey 1942, Fig. 2), perhaps due to the reduction of its wintering habitat in Mexico (Austin 1968), where the human population is burgeoning. I observed a female at ONWR west of Woods Bottom Pond and on the Green River floodplain 600 m southwest of the Green River bridge at Ouray (Fig. 2). At least 10 sightings were made in the desert region of Uintah County 15 May–4 June or later that month and from 9 August or later that month to 6 September 1950, 1957, 1974, 1975, 1977, and 1980–1982 (Anonymous 1977, Behle 1981, Leppert 1982, Beidleman, in litt., D. Chure, in litt.).

Blue Grosbeak (*Guiraca caerulea*). Now well distributed in the low valleys of northern Utah due to the recent northward extension of its range (Hayward et al. 1976). Twomey (1942) did not see it in 1937. I observed it at the confluence of Bitter Creek and White River, along White River between the West Fork of Saddle Tree Draw and MFB (Route 15), at sites 9 and 10, along Road K, at SLWMA, ONWR, and the north end of Split Mountain Campground, Dinosaur National Monument (Figs. 1–2). More than 12 other sightings were made 5 June–12 September 1950, 1951, 1967, 1973–1976, 1980, and 1981 (Behle and Selander 1952, Behle 1981, D. Chure, in litt., D. Chure and L. Ferris, pers. comm.).

Lazuli Bunting (*Passerina amoena*). Hayward et al. (1976) noted that it occurs from early May to early September in Utah, and Behle and Perry (1975a) indicated that it exists there 17 April–15 September. I observed it in riparian habitat of Uintah County 30 April–26 September (Fig. 2).

Indigo Bunting (*Passerina cyanea*). An adult male bird atop a box elder tree at Cub Creek in Dinosaur National Monument was observed by J. C. Oliphant (a federal bird bander) and M. Oliphant 7 July 1976 (D. Chure, in litt.). A male calling from a branch of a cottonwood tree about 9 m above the ground along Green River approximately 7 km southwest of Ouray was observed by S. Madsen (pers. comm.) for about 10 minutes 27 May 1980.

Green-tailed Towhee (*Pipilo chlorurus*). Except for Twomey's (1942) observations, only one published record of it in the desert region of northeastern Utah had been made (Behle 1981). It is evidently less common now (Fig. 2) than in 1937 (Twomey 1942). Since 1937 in the desert region of Uintah County, more than 11 sightings were made from April to 6 June and on 14 August and another day or days that month in 1943, 1945, 1951, 1975, 1976, 1981, and 1982 (Anonymous 1977, Behle 1981, Leppert 1982, Beidleman, in litt., D. Chure, in litt.). I observed it at site 9 and on the Green River floodplain 100–700 m southwest of the Green River bridge at Ouray (Fig. 1).

Rufous-sided Towhee (*Pipilo erythrophthalmus*). Twomey (1942) did not see it between May and mid-September in 1937, but I observed it many times during its nesting season (Fig. 2). More than 26 other sightings were made in the desert region of Uintah County 18 March–5 September in 1895, 1942, 1947, 1950, 1951, 1956, 1957, 1965–1967, 1973–1975, 1978, and 1982 (Behle 1981, Leppert 1982, Beidleman, in litt., D. Chure, in litt.).

American Tree Sparrow (*Spizella arborea*). Apparently less common now (Fig. 2) than in the early and mid-1950s when M. L. Killpack and associates on Audubon Christmas counts in an area including part of western Uintah County saw 100 birds in 1951 (Killpack et al. 1952), 211 in 1952 (Crittenden et al. 1953), 81 in 1953 (Killpack et al. 1954), 459 in 1954 (Crittenden et al. 1955), 73 in 1955 (Killpack et al. 1956), and 178 in 1956 (Killpack 1957). They observed only 6 in 1957 (Killpack 1958) and 3 in 1958 (Killpack 1959). On an Audubon bird count in the Jensen area 26 December 1982, 10 were seen (D. Chure and L. Ferris, pers. comm.).

Chipping Sparrow (*Spizella passerina*). Evidently not as common in the desert region of Uintah County (Fig. 2) as in 1937, when Twomey (1942) saw flocks comprising as many as 200 birds. At least 9 sightings were made there by other observers 15 May–23 June and 5 August–30 September in 1949, 1957, 1973, 1974, and 1982 (Behle 1981, Leppert 1982, Beidleman, in litt., D. Chure, in litt.). I sighted the species at site 9 and at SLWMA (Fig. 2).

Brewer's Sparrow (*Spizella breweri*). In this study, it was observed only as late as 19 September (Fig. 2). Twomey (1942) observed it until 30 September, when his investigation ended.

Vesper Sparrow (*Pooecetes gramineus*). Hayward et al. (1976) stated that it is a common species in Utah that nests in sagebrush habitat, particularly in high valleys, where it exists in the same habitat as the equally common Brewer's Sparrow. Hayward (1967) remarked that it breeds throughout the upper Colorado River basin, where it prefers to nest in desert shrubs of low to medium height. Behle (1981) indicated that in northeastern Utah, it breeds from elevations 1980–3200 m. Twomey (1942) stated that it was the "most uniformly distributed bird" in the Uinta Basin in 1937. Fledglings barely able to fly were observed 24 km southwest of Vernal 12 June 1937 (Twomey 1942).

Most of my observations of the species were made in April. Spring sightings not made then occurred at site 11 30 March 1978, site 12 14 May 1980, and site 14 13 and 14 June 1979 (Figs. 1–2). At site 14, it was not seen after 14 June or before 13 June and did not nest there. I did not see it between 14 June and 14 September (Fig. 2). One was collected 16 km south of Ouray 27 July 1967, however (Behle 1981). On the Roan Plateau of western Colorado between 2440 and 3050 m, it was the most common species in snowberry-sagebrush habitat (Cook 1981). Brewer's Sparrow was sparse there (Cook 1981). Within the arid region of northeastern Utah and northwestern Colorado during summer, Brewer's Sparrows frequent deserts and Vesper Sparrows prefer mountains. In the desert region of Uintah County, the species is less common now (Fig. 2) than it was in 1937, when it nested there (Twomey 1942).

Black-throated Sparrow (*Amphispiza bilineata*). Hayward (1967) noted that in the upper Colorado River valley it occurred 2 May–mid-August in areas where shadscale and low rabbitbrush predominate. It was reported at the federal oil shale tracts U-a and U-b in shadscale, juniper, and riparian habitats from April to August of 1975 and 1976 (Anonymous 1977). At T10S, R25E, Sec. 19, Strong (Olsen 1973) saw two in desert scrub habitat sometime between 24 May and 26 June 1973. At Dinosaur National Monument, it was sighted at Green River Campground by both Argante 1 June 1973 and N. Stephan 7 June 1973, atop a sagebrush at Prophecy in Stone southeast of the Dinosaur Quarry Visitor Center by J. Graham 10 July 1979, and on the Red Rock Nature Trail (possibly in the desert region of Uintah County) by B. Ingber 12 August 1981 (D. Chure, in litt.).

In this study avian populations were very small (unpubl. data) at site 12 (Fig. 1), but in June 1979 several immature and adult Black-throated Sparrows constituted the most common species there. Apparently they nested there or nearby. None were observed along another transect at site 14 (Fig. 1) existing along a wash with vegetation dominated by greasewood. It was seen once in greasewood habitat in Sand Wash (site 10, Fig. 1), however. Although it was observed during the summers of 1978–1980 in the present study, it was not seen in summer 1981. Uintah County is near the northern boundary of its range, and in 1981 apparently not many birds migrated as far north as White River in Uintah County. Perhaps Lloyd and Twomey (Twomey 1942) did not observe it in 1937 because its range did not extend as far north then as it generally has in recent years.

Sage Sparrow (*Amphispiza belli*). Reported to be uncommon (Behle and Perry 1975a,b, Behle 1981), "rather uncommon" (Hayward 1967), or sparse (Hayward et al. 1976) in Utah. In western Colorado, it is reported to be a common resident of sagebrush habitat (Bailey and Niedrach 1965), and I found it to be the same in the desert scrub habitat of Uintah County (Fig. 2). It is at least as common there now (Fig. 2) as in 1937 (Twomey 1942) and is more prevalent there than in Utah generally (Hayward 1967, Behle and Perry 1975a, Hayward et al. 1976, Behle 1981).

During their nesting period, Sage Sparrows at Kennedy Basin (40°05′N, 109°17′W) 18 km northwest of Bonanza, preferred to inhabit what Green (1981) considered to be mixed shrub–sand dune communities. He noted that sagebrush–greasewood and saltbush–bud sagebrush communities adjacent to a mixed shrub–sand dune community were seldom used by the birds. Green (1981) indicated that it selected habitat containing large, sparsely distributed shrubs where there was little forb and litter cover. All ground nests were in depressions beneath clumps of rabbitbrush and elevated nests were in shrubs at a mean height of 26 cm (Green 1981). Over 1979 and 1980, 95% of the young fledged (Green 1981). Miller (1968) stated that during late summer, Sage Sparrows congregate while experiencing their postnuptial molt and that flocks wander in fall. Green (1981) remarked that small groups of juveniles from supposed first clutches flocked in July and joined adults and presumed juveniles from second clutches in late August. However, these behaviors do not constitute major flocking among the species. That occurs in October when large congregations are formed, particularly along washes where greasewood predominates. Large migratory flocks also occur in the deserts of Uintah County in March. Of the migrant sparrows that nest in the desert region of Uintah County, the Sage Sparrow is the first to arrive and the last to leave (Fig. 2).

Lark Bunting (*Calamospiza melanocorys*). More than 26 sightings were made in Uintah County during 15–31 May and throughout June in 1950, 1952, 1953, 1966, 1979, and 1982 (Killpack 1951, Porter and Egoscue 1954, Behle and Ghiselin 1958, Anonymous 1977, Kingery 1979b, Behle 1981, Leppert 1982, Fig. 2).

At Kennedy Basin (40°05′N, 109°17′W), 18 km northwest of Bonanza, Lark Buntings arrived on 16 May and departed on 6 August in 1979 and arrived 14 May and departed 10 August in 1980 (Johnson 1981). The birds existed at a density of about 0.6/ha at a male to female ratio of approximately 3:1. Excess males served as nest helpers in feeding nestlings (Johnson 1981). In 1979 all nests were confined to one area, but in 1980 nests were clumped in groups of four or five. In 1980, all nests were destroyed by trucks involved in oil and natural gas operations (Johnson 1981). At Kennedy Basin the species utilized open, low desert shrub habitat (average height 6–30 cm) 86% of the time (Johnson 1981). Males frequented greasewood habitat 10 times more often than females (Johnson 1981).

Savannah Sparrow (*Passerculus sandwichensis*). Much less common (Fig. 2) than it was in 1937 (Twomey 1942). I observed it along Green River adjacent to desert scrub habitat approximately 250 m downstream from the Green River bridge at Dinosaur National Monument, near White River about 1.3 km southwest of MFB, at SLWMA, site 1, and along the northwest shore of Pelican Lake near a diked marsh (Figs. 1–2). Utah Field Ornithologists observed one bird at ONWR and Pelican Lake 15–16 May 1982 (Leppert 1982).

Song Sparrow (*Melospiza melodia*). Twomey (1942) stated that during 7 May–30 June 1937, it bred in dense willows along Green River and its tributaries in the vicinity of Jensen. Since 1937 there has been no specific sighting record of it between April and September in the desert region of Uintah County (Fig. 2) except 15 May 1982 at Josie Morris Cabin, Dinosaur National Monument (possibly in the desert region of Uintah County; Leppert 1982). Behle (1981) noted that the Song Sparrow often wintered in desert scrub habitat. I performed extensive transect surveys (unpubl. data) in that habitat in all seasons and saw it there only once. In the desert region of Uintah County, it prefers thickets along marshes (particularly at SLWMA) but also occurs near streams and lakes.

Lincoln's Sparrow (*Melospiza lincolnii*). One was observed in front of the headquarters of Dinosaur National Monument 5 May 1956 by J. M. Good, who had heard several birds some weeks before that date in Bug Draw above the headquarters (Beidleman, in litt.). The species was sighted at the confluence of White and Green rivers 22 March 1967 (Behle 1981). Specimens were collected at ONWR 2 April 1963 and at White River 8 km east of Bonanza 26 May 1974 (Behle 1981). In 1937, birds were observed at what is now SLWMA during 1–15 May and 1–30 September, particularly 20 September (Twomey 1942). It is less common now (Fig. 2). I observed it 600 m southwest of MFB, twice 400–500 m south of MFB, at SLWMA, along the north shore of Pelican Lake, and three times at ONWR (Figs. 1–2).

White-throated Sparrow (*Zonotrichia albicollis*). An immature was banded at ONWR by C. Clemens and M. Lange in November 1982 (M. Lange, pers. comm.).

White-crowned Sparrow (*Zonotrichia leucophrys*). I saw it 14 September–21 May (Fig. 2). Hayward et al. (1976) noted that *Z. l. oriantha* is the breeding subspecies in Utah and that *Z. l. gambelii* is more common than *Z. l. oriantha* in winter. However, in the desert region of Uintah County, *Z. l. oriantha* was always more common.

Harris' Sparrow (*Zonotrichia querula*). Killpack (1958) saw 15 on 31 December 1957, but they probably were members of a flock in Duchesne County that was seen 28 December 1957 (Killpack and Hayward 1958). D. Thompson (D. Chure, in litt.) observed one at Dinosaur Quarry Residential Area 8 May 1965. I observed one among a small flock of Dark-eyed Juncos in cottonwoods near White River about 1.7 km southwest of MFB (site 9) and one twice at site 1 (Fig. 2).

Dark-eyed Junco (*Junco hyemalis*). Although it is common in the desert region of Uintah County (Fig. 2), it is evidently not as abundant as it was in 1937 (Twomey 1942). It was observed at Dinosaur National Monument as late as 1 June in spring and as early as 22 September in fall (Beidleman, in litt., D. Chure, in litt.). On an Audubon Christmas bird count in the Jensen area, 58 *J. h. hyemalis* and 48 *J. h. montanus* were reported 26 December 1982 (D. Chure and L. Ferris, pers. comm.). Twomey (1942) indicated that in 1937 the subspecies *J. h. caniceps* was abundant in lowland riparian areas throughout May and during 25–30 September. Four members of that subspecies were seen on Green River south of Jensen 5 August 1937 (Twomey 1942). In this study *J. h. caniceps* was not seen in the desert region of Uintah County. It was the only subspecies that I observed on the Roan Plateau of western Colorado (el. 2440–3050 m) during summer (Cook 1981).

McCown's Longspur (*Calcarius mccownii*). One was reported at Green River Campground, Dinosaur National Monument, by N. Stephan 7 June 1973 (D. Chure, in litt.).

Icteridae

Red-winged Blackbird (*Agelaius phoeniceus*). In Uintah County it is much less prevalent in winter than during other seasons.

Eastern Meadowlark (*Sturnella magna*). One was reportedly heard by H. G. Troester (pers. comm.) at ONWR in 1981.

Western Meadowlark (*Sturnella neglecta*). Twomey (1942) noted that it began to migrate south from the Uinta Basin by 30 September 1937. It occurs throughout the year in Uintah County (Fig. 2) and congregates where livestock are fed in winter. It is at least as abundant now (Fig. 2) as it was in 1937 (Twomey 1942).

Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*). Two were seen in the Jensen area unusually late (Fig. 2) 26 December in 1982 (D. Chure and L. Ferris, pers. comm.).

Brewer's Blackbird (*Euphagus cyanocephalus*). Although common, it is apparently less abundant (Fig. 2) than it was in 1937 (Twomey 1942). Its occurrence in Uintah County during winter is limited to localized flocks at farm yards such as the one along Utah Highway 149 (Road B) about 1 km north of its junction with U.S. Highway 40 (Fig. 1).

Great-tailed Grackle (*Quiscalus mexicanus*). One was sighted at PWA 12 May 1982 by D. Zalunardo and S. Madsen (pers. comm.).

Common Grackle (*Quiscalus quiscula*). In May it has been seen on the grounds of the Utah Field House of Natural History (Behle 1981, Kingery 1981c, Fig. 2) and at SLWMA (Leppert 1982).

Brown-headed Cowbirds (*Molothrus ater*). Apparently more common now (Fig. 2) than in 1937 (Twomey 1942).

Northern Oriole (*Icterus galbula*). Although common, it is less abundant (Fig. 2) than in 1937 when Twomey saw large migratory flocks (Twomey 1942). Twomey (1942) commented that in 1937 Northern Orioles were tame. Now they are very wary. I did not see the species after 25 August (Fig. 2), but in 1937 it emigrated from the Uinta Basin from the first week of August to mid-September (Twomey 1942).

Scott's Oriole (*Icterus parisorum*). Reported on or near the federal oil shale tracts U-a and U-b in sagebrush-greasewood, riparian, and juniper habitats in June and August 1975 and 1976 (Anonymous 1977). M. Pasho (D. Chure, in litt.) sighted it at Split Mountain Boat Ramp, Dinosaur National Monument, in June 1981. A. R. Johnson and B. H. Green (White et al. 1983) saw four to five 12–16 km west of the Colorado border 11–14 August 1979.

Fringillidae

Rosy Finch (*Leucosticte arctoa*). J. M. Good (Beidleman, in litt.) saw a large flock of the gray-crowned subspecies (*L. a. tephrocotis*) at Split Mountain Campground, Dinosaur National Monument, 1 November 1956. In greasewood, shadscale, juniper, and riparian habitats on or near the federal oil shale tracts U-a and U-b during 1975 and 1976, this subspecies was observed in December and February (Anonymous 1977). Hayward (1967) collected two representatives of the black subspecies (*L. a. atrata*) near Randlett 6 May 1950 and two from a large flock north of Vernal 13 May 1961. T. Tornow (pers. comm.) sighted that subspecies in Johnson Bottom of ONWR in January and February 1979 but did not see it at ONWR during 1980–1982. In greasewood, shadscale, juniper, and riparian habitats on or near the federal oil shale tracts U-a and U-b during 1975 and 1976, *L. a. atrata* were observed from December to April (Anonymous 1977).

Cassin's Finch (*Carpodacus cassinii*). Twomey (1942) observed seven in cottonwood snags immediately south of the Ashley Creek marshes at what is now SLWMA. I observed one with a small flock of House Finches at site 4 (Figs. 1–2). Utah Field Ornithologists saw one at Split Mountain Campground, Dinosaur National Monument, and one in a Vernal park 15–16 May 1982 (Leppert 1982).

House Finch (*Carpodacus mexicanus*). Twomey (1942) stated that in 1937 it was very abundant and was probably the widest ranging bird in the Uinta Basin because it existed from river floodplains and desert badlands to timberline of the Uinta Mountains. Hayward (1967) noted that it is one of the most common birds in the upper Colorado River basin. More than 27 sightings of it were made in the desert region of Uintah County 18 March–October and 29 December 1949, 1950, 1956–1958, 1961, 1966, 1973–1976, and 1982 (Behle and Ghiselin 1958, Killpack 1959, Anonymous 1977, Behle 1981, Leppert 1982, Biedleman, in litt., D. Chure, in litt.). It was less prevalent during this study (Fig. 2) than it was in earlier decades (Twomey 1942, Behle 1981, Beidleman, in litt.). I observed it 26 January (Fig. 2), although relatively few birds winter in the northern portion of the upper Colorado River basin (Hayward 1967).

Common Redpoll (*Carduelis flammea*). At site 4, I saw a male with several Tree Sparrows eating the seeds of *Kochia sp.* 29 December 1978 (Figs. 1–2).

Pine Siskin (*Carduelis pinus*). Less common (Fig. 2) than it was in 1937 (Twomey 1942). I observed it only 1 October–1 January (Fig. 2); the following observations were made at other times. Twomey (1942) heard or saw many migrating birds during the first two weeks of May and 21–30 September 1937. At Dinosaur National Monument, it has been seen 1–14 August (Beidleman, in litt., D. Chure, in litt.). It was collected at ONWR 9 April 1963 and 20 March 1966 (Behle 1981). Twenty were seen outside the Utah Field House of Natural History 15 May 1982 (Leppert 1982, D. Chure, pers. comm.).

Lesser Goldfinch (*Carduelis psaltria*). In Vernal Twomey (1942) observed a male in a private flower garden 22 July 1937 and a male and two females 10 and 12 August 1937. In Dinosaur National Monument, Argante saw it at Green River Campground 1 June 1973, J. Starbler sighted it at Cub Creek 1 and 23 June 1973, N. Howk and B. Ingber saw three in greasewood brush near Josie Morris Cabin 18 July 1980 and 10 pairs at Cub Creek 14 August 1981, and J. Freilich observed it at Box Canyon near Josie Morris Cabin 21 August 1979 (D. Chure, in litt.).

American Goldfinch (*Carduelis tristis*). More than 26 sightings were made in the desert region of Uintah County 18 March–28 August 1945, 1949, 1957, 1963, 1966, 1967, 1973–1976, and 1980–1982 (Behle and Ghiselin 1958, Anonymous 1977, Behle 1981, Leppert 1982, Beidleman, in litt., D. Chure, in litt.). Twomey (1942) believed that by 30 September 1937, almost all of the American Goldfinches that summered in the Uinta Basin had emigrated south. Contrary to what Twomey (1942) and Behle and Perry (1975a) reported for the Uinta Basin and Utah, respectively, the American Goldfinch is as common in winter as during other seasons in the desert region of Uintah County (Fig. 2). I observed it on eight different days in January. From 11 to 191 individuals were seen in late December 1952–1958 in an area including western Uintah County (Crittenden et al. 1953, 1955, Killpack 1957, 1958, 1959, Killpack et al. 1954, 1956), and on an Audubon Christmas count in the Jensen area 73 birds were observed 26 December 1982 (D. Chure and L. Ferris, pers. comm.).

Evening Grosbeak (*Coccothraustes vespertinus*). Seen in an area including a western portion of Uintah County 31 December 1953 (3, Killpack et al. 1954) and 29 December 1955 (2, Killpack et al. 1956). In Dinosaur National Monument, R. W. Horton saw 10 at Green River Campground 27 January 1964 and at Dinosaur Quarry Residential Area, W. G. Truesdell observed 80 on 17 February and 17 March 1974, 20 on 3 March 1974, and an unspecified number later in 1974 until 1 May (D. Chure, in litt.). M. L. Perry (pers. comm.) observed the species on the grounds of the Utah Field House of Natural History in Vernal during at least one winter in the 1970s. Utah Field Ornithologists saw one at Josie Morris Cabin, Dinosaur National Monument, and 10 at Vernal parks 15–16 May 1982 (Leppert 1982).

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1982. Thirty-fourth supplement to the American Ornithologists' Union check-list of North American birds. Auk 99:1CC–16CC.

ANONYMOUS. 1977. Terrestrial vertebrates. Pages 79–203 *in* Final environmental baseline report, federal prototype oil shale leasing program, Tracts U-a and U-b, Utah, White River Shale Project. VTN Colo., Inc, Sec. IV. 458 pp.

AUSTIN, O. L. 1968. *Pheucticus melanocephalus maculatus* (Audubon), black-headed grosbeak. Pages 58–67 *in* O. L. Austin, Jr., ed., Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Dover Publ., Inc., New York. Pt. 1:1–602.

BAILEY, A. M., AND A. J. NIEDRACH. 1965. Birds of Colorado. Denver, 2 vols. 895 pp.

BEHLE, W. H. 1966. Noteworthy records of Utah birds. Condor 68:396–397.

_____. 1981. The birds of northeastern Utah. Utah Mus. Nat. Hist., Occasional Publ. 2, Univ. of Utah, Salt Lake City. 136 pp.

BEHLE, W. H., AND J. GHISELIN. 1958. Additional data on the birds of the Uinta Mountains and Basin of northeastern Utah. Great Basin Nat. 18:1–22.

BEHLE, W. H., AND M. L. PERRY. 1975a. Utah birds. Utah Mus. Nat. Hist., Univ. of Utah, Salt Lake City. 143 pp.

_____. 1975b. Raptor study of Utah oil shale area. Pages 1–149 *in* R. W. Baumann, R. N. Wingett, W. H. Behle, W. F. Sigler, G. W. Workman, and M. L. Perry, eds., Studies for wildlife on energy areas. Utah State Dept. Nat. Res., Div. Wildl. Res., Salt Lake City.

BEHLE, W. H., AND R. K. SELANDER. 1952. New and additional records of Utah birds. Wilson Bull. 64:26–32.

BENT, A. C. 1961. *Falco peregrinus anatum* Bonaparte, duck hawk. Pages 43–67 *in* A. C. Bent, ed., Life histories of North American birds of prey. Dover Publ., Inc., New York, Pt. 2. 482 pp. + 92 plates.

_____. 1962a. *Pisobia bairdi* (Coues), Baird sandpiper. Pages 193–202 *in* A. C. Bent, ed., Life histories of North American shore birds. Dover Publ., Inc., New York, Pt. 1. 420 pp. + 55 plates.

_____. 1962b. *Limosa fedoa* (Linnaeus), marbled godwit. Pages 277–289 *in* A. C. Bent, ed., Life histories of North American shore birds. Dover Publ., Inc., New York, Pt. 1. 420 pp. + 55 plates.

_____. 1962c. *Totanus melanoleucus* (Gmelin), greater yellow-legs. Pages 321–336 *in* A. C. Bent, ed., Life histories of North American shore birds. Dover Publ., Inc., New York, Pt. 1. 420 pp. + 55 plates.

_____. 1963a. *Tyrannus verticalis* Say, Arkansas kingbird. Pages 57–70 *in* A. C. Bent, ed., Life histories of North American flycatchers, larks, swallows, and their allies. Dover Publ., Inc., New York. 555 pp. + 70 plates.

_____. 1963b. *Myiarchus cinerascens cinerascens* (Lawrence), ash-throated flycatcher. Pages 128–136 *in* A. C. Bent, ed., Life histories of North American flycatchers, larks, swallows, and their allies. Dover Publ., Inc., New York. 555 pp. + 70 plates.

_____. 1963c. *Sayornis saya saya* (Bonaparte), Say's phoebe. Pages 166–173 *in* A. C. Bent, ed., Life histories of North American flycatchers, larks, swallows, and their allies. Dover Publ., Inc., New York. 555 pp. + 70 plates.

———. 1963d. *Empidonax hammondi* (Xantus), Hammond's flycatcher. Pages 225–233 *in* A. C. Bent, ed., Life histories of North American flycatchers, larks, swallows, and their allies. Dover Publ., Inc., New York. 555 pp. + 70 plates.

———. 1963e. *Empidonax wrighti* Baird, Wright's flycatcher. Pages 233–241 *in* A. C. Bent, ed., Life histories of North American flycatchers, larks, swallows, and their allies. Dover Publ., Inc., New York. 555 pp. + 70 plates.

———. 1964a. *Dryobates villosus monticola* Anthony, rocky mountain hairy woodpecker. Pages 35–37 *in* A. C. Bent, ed., Life histories of North American woodpeckers. Dover Publ., Inc., New York. 334 pp. + 39 plates.

———. 1964b. *Dryobates pubescens leucurus* (Hartlaub), Batchelder's woodpecker. Pages 51–52 *in* A. C. Bent, ed., Life histories of North American woodpeckers. Dover Publ., Inc., New York. 334 pp. + 39 plates.

———. 1964c. *Sphyrapicus varius nuchalis* Baird, red-naped sapsucker. Pages 141–150 *in* A. C. Bent, ed., Life histories of North American woodpeckers. Dover Publ., Inc., New York. 334 pp. + 39 plates.

BREED, W. J. 1976. Canyons of wonder, rivers of time. Pages 296–323 *in* S. L. Fishbein, ed., Our continent, a natural history of North America. Nat. Geog. Soc., Wash., D.C. 398 pp.

COOK, A. G. 1981. Terrestrial fauna. Pages 3-1–3-35 *in* Naval oil shale reserves, biological resources baseline report. TRW Energy Engineering Div., McLean, Virginia.

CRITTENDEN, D. N., R. COOK, R. HARRISON, AND M. L. KILLPACK. 1953. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 7:174.

CRITTENDEN, D. N., L. FAUSETT, M. L. KILLPACK, F. LARSEN, AND J. C. PERCEVAL. 1955. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 9:213.

GRAHAM, E. H. 1937. Botanical studies in the Uinta Basin of Utah and Colorado. Ann. Carnegie Mus. 26:1–432.

GREEN, B. H. 1981. Habitat selection and utilization by sage sparrows (*Aimphispiza belli*) in a cold desert mixed shrub community. Unpublished thesis. Brigham Young Univ., Provo, Utah, 24 pp.

HAYWARD, C. L. 1966. New and unusual bird records from Utah. Condor 68:305–306.

———. 1967. Birds of the upper Colorado River basin. Brigham Young Univ. Sci. Bull., Biol. Ser. 9(2):1–64.

HAYWARD, C. L., C. COTTAM, A. M. WOODBURY, AND H. H. FROST. 1976. Birds of Utah. Great Basin Nat. Memoirs 1, Brigham Young Univ. Press, Provo, Utah. 229 pp.

JOHNSON, A. R. 1981. Habitat utilization by lark buntings (*Calamospiza melanocorys*) in a cold desert mixed shrub community. Unpublished thesis. Brigham Young Univ., Provo, Utah. 16 pp.

KILLPACK, M. L. 1951. Lark bunting in Uintah [sic] Basin, Utah. Condor 53:99.

———. 1957. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 11:215.

———. 1958. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 12:225–226.

———. 1959. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 13:238.

KILLPACK, M. L., A. COLLATZI, AND F. LARSEN. 1952. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 6:159.

KILLPACK, M. L., D. N. CRITTENDEN, A. COLLATZI, R. HARRISON, AND F. LARSEN. 1954. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 8:206.

KILLPACK, M. L., AND C. L. HAYWARD. 1958. New and unusual records of birds from the Uinta Basin. Great Basin Nat. 18:23–25.

KILLPACK, M. L., D. HEED, AND J. PERCEVAL. 1956. Christmas bird count, Roosevelt, Utah. Aud. Field Notes 10:208.

KINGERY, H. E. 1976. The nesting season, June 1–July 31, 1976. Mountain west. Amer. Birds 30:982–985.

———. 1979a. Continental survey. The winter season, December 1, 1978–February 28, 1979. Mountain west. Amer. Birds 33:300–302.

———. 1979b. Continental survey. The spring migration, March 1–May 31, 1979. Mountain west. Amer. Birds 33:793–795.

———. 1980a. Continental survey. The spring migration, March 1–May 31, 1980. Mountain west. Amer. Birds 34:800–803.

———. 1980b. Continental survey. The nesting season, June 1–July 31, 1980. Mountain west. Amer. Birds 34:914–918.

———. 1981a. Continental survey. The autumn migration, August 1–November 30, 1980. Mountain west. Amer. Birds 35:208–211.

———. 1981b. Continental survey. The winter season, December 1, 1980–February 28, 1981. Mountain west. Amer. Birds 35:321–323.

———. 1981c. Continental survey. The spring migration, March 1–May 31, 1981. Mountain west region. Amer. Birds 35:846–849.

———. 1981d. Continental survey. The nesting season, June 1–July 31, 1981. Mountain west region. Amer. Birds 35:963–966.

———. 1982. Continental survey. The spring migration, March 1–May 31, 1982. Mountain west. Amer. Birds 36:877–880.

———. 1983. Continental survey. The spring migration, March 1–May 31, 1983. Mountain west. Amer. Birds 37:895–898.

LEPPERT, M. 1982. UFO spring trip records 151 species. Black Rosy Finch 2:5–9.

MILLER, A. H. 1968. *Amphispiza belli nevadensis* (Ridgway), northern sage sparrow. Pages 1004–1013 *in* O. L. Austin, Jr., ed., Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Dover Publ., Inc., New York. Pt. 2:603–1248.

OLSEN, P. F. 1973. Wildlife resources of the Utah oil shale area. Publ. 74-2, State of Utah Dept. Nat. Res., Div. Wildl. Res., Salt Lake City. 147 pp.

PEDERSON, J. C., AND D. H. NISH. 1975. The band-tailed pigeon in Utah. Publ. 75-1, Utah State Dept. Nat. Res., Div. Wildl. Res., Salt Lake City. 75 pp.

Porter, R. D., and J. Egoscue. 1954. The lark bunting in Utah. Wilson Bull. 66:219-221.

Porter, R. D., and C. M. White. 1973. The peregrine falcon in Utah, emphasizing ecology and competition with prairie falcon. Brigham Young Univ. Sci. Bull., Biol. Ser. 18(1):1-74.

Richards, G. L., and C. M. White. 1963. Common crow nesting in Utah. Condor 65:530-531.

Sangster, M. E. 1976. Migration and ecology of waterfowl on Ouray National Wildlife Refuge, Utah. Unpublished thesis. Univ. of Missouri, Columbia. 91 pp.

______. 1977. Spring waterfowl migration in the Uinta Basin of northeastern Utah. Great Basin Nat. 37:274-278.

Scott, O. K. 1965. Regional reports. Fall migration, August 16-November 30, 1964. Great Basin, central Rocky Mountain region. Aud. Field Notes 19:63-64.

______. 1968. Regional reports. Spring migration, April 1, 1968-May 31, 1968. Great Basin, central Rocky Mountain region. Aud. Field Notes 22:560-562.

______. 1969. Regional reports. Fall migration, August 16, 1968-November 30, 1968. Great Basin, central Rocky Mountain region. Aud. Field Notes 23:86-87.

Terres, J. K. 1980. The Audubon Society encyclopedia of North American birds. Alfred A. Knopf, New York. 1109 pp.

Tullsen, H. 1908. A note on the spring migration, 1901, at Leland, Uncompahgre Ute Indian Reservation, Utah. Wilson Bull. 20:100.

Twomey, A. C. 1942. The birds of the Uinta Basin, Utah. Ann. Carnegie Mus. 28:341-490.

______. 1944. A correction of identification of sandpipers. Condor 46:90.

Welsh, S. L., and G. Moore. 1973. Utah plants, tracheophyta. Brigham Young Univ. Press, Provo, Utah. 474 pp.

Weston, F. M. 1964. *Polioptila caerulea caerulea* (Linnaeus), blue-gray gnatcatcher. Pages 344-364 *in* A. C. Bent, ed., Life histories of North American thrushes, kinglets, and their allies, Dover Publ., Inc., New York. 452 pp. + 51 plates.

White, C. M., G. D. Lloyd, and G. L. Richards. 1965. Goshawk nesting in the upper sonoran in Colorado and Utah. Condor 67:269.

White, C. M., H. H. Frost, D. L. Shirley, G. M. Webb, and R. D. Porter. 1983. Bird distributional and breeding records for southeastern Idaho, Utah, and adjacent regions. Great Basin Nat. 43:717-727.

PLANT NUTRIENT LEVELS ON TWO SUMMER RANGES IN THE RIVER OF NO RETURN WILDERNESS AREA, IDAHO

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Abstract.— Monthly percent nutrient and moisture levels of plant species on two summer ranges in the River of No Return Wilderness Area of Idaho were determined. *Festuca idahoensis* exhibited the highest average crude protein content of graminoids on both study areas. *Achillea millefolium* and *Balsamorhiza saggittata* at Rush Point and *Trifolium* spp. and *Achillea millefolium* at Cold Meadows possessed the highest mean crude protein content of the forbs examined. Grasses exhibited greater average seasonal levels of crude fiber, and forbs generally contained significantly larger levels of Ca, P, and moisture.

Nutrient data for summer range plants in the mountainous region of south central Idaho are lacking. Claar (1973) presented information concerning winter nutrient trends for browse species in the River of No Return Wilderness Area (formerly the Idaho Primitive Area) but, to our knowledge, no data exist for this area relative to graminoids and forbs on summer ranges.

The quality of summer forage has been demonstrated to have an effect on body condition and reproductive capacity of wild herbivores (Verme 1963, Snider and Asplund 1974, Pederson and Harper 1978). Deficiencies in available plant nutrients are common on western ranges (Cook and Harris 1968) and have led to studies of the nutritional properties of forage plants (Skovlin 1967). Such information can be used to estimate the seasonal nutritional adequacy of plants in animal diets and can be used to implement better management practices.

Study Sites

The study was conducted in the Big Creek Ranger District, River of No Return Wilderness Area, Idaho. A description of the Big Creek drainage is provided by Hornocker (1970). Two types of summer range utilized by wild ungulates were examined.

The Cold Meadows (elev. 2142 m) site was an example of the mountain meadow range type. Meadow vegetation appears to have developed through normal processes of hydroseral succession, with the soils being maintained in a saturated or near saturated condition (Wing 1969). Vegetation within the meadow exhibited a predominance of sedges, with a wide variety of grasses and forbs. Hydromorphic and alluvial soils predominate, but sandy loams occur along the outer meadow edges (Hayden-Wing 1980).

The Rush Point (elev. 1890 m) site represented the sagebrush (*Artemisia tridentata*)-bunchgrass association typical of the southeast-facing slopes used by wild ungulates in the area. Perennial plants dominated the biotic community and occupied soils derived from basalt, granite, sedimentary deposits, and metamorphosed variations of these materials (Mueggler and Harris 1969).

Methods

The botanical communities of the two study sites were compared using Jaccard's (1912) community coefficient. The resulting index value of 22% indicated each site exhibited little similarity in plant composition.

Each study area was visited according to a monthly schedule: Cold Meadows 12–19 June, 17–24 July, and 14–21 August; Rush Point 1–8 June, 1–8 July, and 1–8 August 1977. Plant biomass was determined monthly at each area using the calibrated weight-estimate method (Tadmor et al. 1975). Preliminary sampling in 1976 indicated 10, 90 m transects at Cold Meadows and 14 transects at Rush Point were required to be 95% certain the vegetation biomass sampling mean was within 20% of the true mean for the single most abundant plant species at each site (Subcommittee on Range Research Methods of the Agricultural Board 1962:230). A 50 x 50 cm frame was placed every 9 m along a sampling transect; this plot size was used to reduce the "edge effect" encountered when sampling in tall vegetation (Tadmor et al. 1975).

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After every 10 plots, samples of each plant species that had occurred in amounts of one gram or more per plot were estimated by weight, clipped, weighed to the nearest gram, stored, and returned to the laboratory. All plants were oven dried at 64 C for 72 hrs, weighed, and assessed for moisture content. The plant samples were then pooled, by individual species, for each month and analyzed for nutrient content.

Plant nitrogen content was determined using the Kjeldahl technique (AOAC 1970); this value was multiplied by 6.25 and crude protein was calculated (AOAC 1970). Crude fiber was determined using the Van Soest (1963) method; phosphorus (P) and calcium (Ca) levels were obtained using the dry ashing procedure (Middleton and Stucky 1954). Analyses were performed at the Plant and Soil Analysis Laboratory, Brigham Young University, Provo, Utah. Average nutrient levels, by month, for each plant "group" (grasses and forbs) within a study area were statistically compared using unpaired t-tests (Steel and Torrie 1980). The measure of significance tested for was P = 0.05.

Results and Discussion

The average (± S.D.) monthly percent nutrient and moisture levels of the 10 plant species exhibiting the highest frequency (75%) of occurrence at Cold Meadows and Rush Point are shown in Tables 1 through 4. The average biomass (kg/ha ± S.D.) available on each site was: Cold Meadows 1870 ± 69, Rush Point 1140 ± 77.

At Cold Meadows the group average crude fiber content of grasses was significantly greater than forb levels in all months (Tables 1 and 2). Group mean crude protein levels were not statistically different during June and July, but August protein content of forbs was significantly greater than grasses. Group average forb Ca, P, and moisture levels were significantly greater than grasses for the entire summer period.

Rush Point grasses exhibited significantly greater group mean crude fiber levels in June and July but were equivalent to forbs in August (Tables 3 and 4). Group average crude protein was the same for both plant categories in July and August, but forbs were

Table 1. Average (± S.D.) monthly percent nutrient and moisture content of grass species exhibiting the highest frequency of occurrence at Cold Meadows, River of No Return Wilderness, 1977–1978.

Species	Crude fiber	Crude protein	Ca	P	Ca:P	Moisture
June						
Agropyron caninum	25 ± 0.2	9 ± 2.0	0.14 ± 0.1	0.06 ± 0.02	2.3:1	61 ± 2
Festuca idahoensis	28 ± 0.1	15 ± 3.4	0.25 ± 0.1	0.09 ± 0.001	2.8:1	60 ± 3
Phleum alpinum	28 ± 0.4	17 ± 2.3	0.18 ± 0.02	0.08 ± 0.02	2.3:1	64 ± 2
Group mean (± S.D.)	27.0 ± 1.7	13.7 ± 4.2	0.19 ± 0.1	0.08 ± 0.02	2.4:1	61.7 ± 2.1
July						
Agropyron caninum	33 ± 1.4	11 ± 1.9	0.14 ± 0	0.07 ± 0.01	2.0:1	59 ± 1.5
Festuca idahoensis	36 ± 1.0	13 ± 1.3	0.19 ± 0.01	0.07 ± 0.003	2.7:1	59 ± 3
Phleum alpinum	34 ± 0.7	9 ± 1.0	0.17 ± 0.04	0.07 ± 0.002	2.4:1	54 ± 2
Group mean	34.3 ± 1.5	11.0 ± 2.0	0.17 ± 0.03	0.07	2.4:1	57.3 ± 2.9
August						
Agropyron caninum	35 ± 0.4	8 ± 1.2	0.14 ± 0.01	0.04 ± 0.01	3.5:1	50 ± 2
Festuca idahoensis	37 ± 0.2	10 ± 1.1	0.20 ± 0.01	0.07 ± 0.002	2.9:1	31 ± 1
Phleum alpinum	34 ± 0.1	7 ± 0.9	0.20 ± 0.2	0.09 ± 0.001	2.2:1	27 ± 2
Group mean	35.3 ± 1.5	8.3 ± 0.03	0.18 ± 0.03	0.07 ± 0.03	2.6:1	36.0 ± 12.3

significantly higher in June. Group average calcium content was significantly higher in forbs in July and August. Group mean P levels were significantly higher in forbs in June, grasses in July, and equivalent in August. Group average moisture content was significantly greater in forbs throughout the summer.

The group average Ca:P ratios for grasses on both study sites were generally consistent throughout the summer. The June Ca:P ratio for Rush Point was dramatically inflated by the 1.15% Ca level reported for *Agropyron spicatum*. This value may be unrealistically high, but no material remained after the initial analysis; hence a reanalysis of the sample was not possible. Calcium:P ratios for forbs generally increased throughout the summer.

The principle wild ungulates observed using the two study areas were bighorn sheep (*Ovis canadensis*) at Rush Point and elk (*Cervus elaphus*) at Cold Meadows. Elk cows and calves were especially prevalent on Cold Meadows.

The summer diet of elk on five mountain meadows in the Cottonwood Creek watershed (of which Cold Meadows is a part) have been reported to consist primarily of forbs, sedges second, grasses third, and shrubs least (Hayden-Wing 1980). Frequency of use of most grass and shrub species were less than 10%, but exceeded 10% for most forb and sedge species. No grass species exceeded 26% frequency of utilization, but several species of forbs, sedges, and shrubs reportedly exceeded 40% (Hayden-Wing 1980).

Forbs composed 44% of the summer (June–August) diet of Big Creek bighorn sheep; shrubs and grasses made up 36% and 20%, respectively. *Agropyron spicatum* (11%), *Achillea millefolium* (11%), *Balsamorhiza saggittata* (10%), *Cercocarpus ledifolius* (9%), *Physocarpus malvalceous* (8%), and *Lupinus sericeus* (6%) were the major species proportionately evident in the diet (J. Bennett pers. comm.).

The adequacy of the nutritional plane in the vegetation will be considered in relation

TABLE 2. Average (± S.D.) monthly percent nutrient and moisture content of forb species exhibiting the highest frequency of occurrence at Cold Meadows, River of No Return Wilderness, 1977–1978.

Species	Crude fiber	Crude protein	Ca	P	Ca:P	Moisture
			June			
Achillea millefolium	22 ± 2.0	20 ± 1.6	0.51 ± 0.16	0.19 ± 1.63	2.7:1	78 ± 5
Erigeron speciosus	18 ± 0.3	19 ± 0.4	0.56 ± 0.13	0.16 ± 0.06	3.5:1	75 ± 3
Fragaria virginiana	17 ± 0.7	16 ± 0.7	0.68 ± 0.13	0.10 ± 0.09	6.8:1	72 ± 3
Penstemon spp.[1]	26 ± 0.7	15 ± 2.0	0.57 ± 0	0.15 ± 0.003	3.8:1	72 ± 2
Potentilla gracilis	19 ± 1.4	20 ± 2.3	0.65 ± 0.1	0.18 ± 0.05	3.6:1	75 ± 3
Senecio serra	22 ± 0.4	14 ± 1.4	0.62 ± 0.04	0.15 ± 0.07	4.1:1	78 ± 2
Trifolium spp.[2]	15 ± 0.7	27 ± 1.2	1.70 ± 0.5	0.44 ± 0.02	3.9:1	70 ± 2
GROUP MEAN (± S.D.)	19.9 ± 3.7	18.7 ± 4.4	0.76 ± 0.4	0.20 ± 0.1	3.8:1	74.3 ± 3.1
			July			
Achillea millefolium	24 ± 1.8	17 ± 0.3	0.90 ± 0.04	0.20 ± 0.01	4.5:1	64 ± 2
Erigeron speciosus	20 ± 1.4	16 ± 0.9	0.65 ± 0.10	0.16 ± 0.03	4.1:1	69 ± 3
Fragaria virginiana	28 ± 16.3	13 ± 1.3	0.85 ± 0.05	0.18 ± 0.03	4.7:1	66 ± 1
Penstemon spp.	33 ± 3.5	9 ± 1.3	0.58 ± 0.03	0.13 ± 0.02	4.5:1	68 ± 3
Potentilla gracilis	17 ± 1.4	16 ± 1.6	0.69 ± 0.25	0.18 ± 0.01	3.8:1	65 ± 2
Senecio serra	29 ± 0.7	10 ± 0.2	0.78 ± 0.17	0.19 ± 0.05	4.1:1	75 ± 5
Trifolium spp.	20 ± 0.9	22 ± 1.2	1.30 ± 0.11	0.40 ± 0.05	3.3:1	55 ± 2
			August			
Achillea millefolium	25 ± 1.2	14 ± 0.9	1.05 ± 0.10	0.20 ± 0.04	5.3:1	58 ± 3
Erigeron speciosus	24 ± 1.0	13 ± 0.4	1.03 ± 0.10	0.20 ± 0.04	5.2:1	58 ± 4
Fragaria virginiana	16 ± 9.0	12 ± 0.5	0.83 ± 0.06	0.18 ± 0.03	4.6:1	52 ± 1
Penstemon spp.	31 ± 2.1	10 ± 0.9	0.92 ± 0.03	0.14 ± 0.002	6.6:1	47 ± 1
Potentilla gracilis	19 ± 1.1	12 ± 1.5	1.07 ± 0.11	0.19 ± 0.01	5.6:1	58 ± 3
Senecio serra	30 ± 0.3	8 ± 0.5	0.91 ± 0.13	0.21 ± 0.04	4.3:1	50 ± 1
Trifolium spp.	27 ± 0.6	14 ± 0.9	1.05 ± 0.06	0.34 ± 0.03	3.1:1	35 ± 3
GROUP MEAN	24.6 ± 5.5	11.9 ± 2.2	0.98 ± 0.1	0.21 ± 0.1	4.7:1	51.1 ± 8.4

[1] Includes *Penstemon procerus* and *P. rydbergii*.
[2] Includes *Trifolium repens* and *T. longipes*.

to the ungulate species observed using the forage. The nutritional requirements of bighorn sheep and elk were equated with the nutritional demands of a domestic sheep (*Ovis* spp.) and a steer (*Bos* spp.), respectively. This comparison may seem questionable, but it provides a qualitative method with which to assess the adequacy of forage plants in meeting the nutritional needs of the wildlife species.

Rush Point

The National Research Council (NRC 1975:44) recommends a minimum 8.9% crude protein in the diet for growth in domestic sheep. On this basis, both forbs and grasses contained sufficient protein to meet requirements during June and July but were declining in August. The NRC (1975:44) recommends a ration containing 0.25–0.30% Ca and 0.24–0.38% P for maintenance in domestic sheep. The forbs and grasses generally exceeded the required Ca levels, but neither group consistently met the P recommendation.

Cold Meadows

Thorne et al. (1976) noted cow elk responded to different levels of nutrition much as do domestic ruminants. Early attainment of large size was postulated to be important in preparing free-ranging elk calves for winter. In their experiment, the only group of elk to gain weight were fed diets containing 13.4–14.5% crude protein. This corresponds closely with the crude protein levels (12.7–16.2%) Papageorgiou (1978) found in forage preferred by red deer in Greece. Forbs at Cold Meadows maintained similar protein levels throughout the summer, but graminoids were deficient. Calcium and P levels, based on NRC (1976:28) requirements for a 300 kg steer (P = 0.18–0.34%, Ca = 0.18–0.42%), were variable—sufficient levels of Ca in forbs and grasses but deficient levels of P in both categories.

Maynard et al. (1979:224) indicated an acceptable ratio of Ca:P to be from 1:1 to 2:1 for farm animals other than poultry. When the proportion reaches about 10:1 problems occur. An excess of Ca interferes with the efficient assimilation of P (Maynard et al. 1979:224). The Ca:P ratios for all plant categories on both sites exceeded the 2:1 ratio but generally never approached the problem level of 10:1.

Chemical analysis indicated grasses exhibited greater average seasonal levels of crude fiber, and forbs generally contained significantly larger levels of Ca, P, and moisture. Crude protein levels declined over the summer but were at sufficient levels during the critical early summer months that are important for newborn, as well as maturing, sheep and elk. Like other herbivores in temperate environments, elk and bighorn sheep must

Table 3. Average (± S.D.) monthly percent nutrient and moisture content of grass species exhibiting the highest frequency of occurrence at Rush Point, River of No Return Wilderness, 1977–1978.

Species	Crude fiber	Crude protein	Ca	P	Ca:P	Moisture
			June			
Agropyron spicatum	36 ± 4.9	15 ± 2.5	1.15 ± 1.24	0.11 ± 0.04	10.5:1	61 ± 2
Festuca idahoensis	35 ± 1.4	13 ± 0.1	0.36 ± 0.09	0.12 ± 0.001	3.0:1	61 ± 2
Koeleria cristata	38 ± 1.2	11 ± 0.5	0.12 ± 0.04	0.08 ± 0.02	1.5:1	57 ± 1
Group mean (± S.D.)	36.3 ± 1.5	13.0 ± 2.0	0.54 ± 0.5	0.10 ± 0.02	5.4:1	59.7 ± 2.3
			July			
Agropyron spicatum	38 ± 3.1	12 ± 2.4	0.51 ± 0.33	0.09 ± 0.01	5.7:1	41 ± 2
Festuca idahoensis	32 ± 7.4	13 ± 3.7	0.21 ± 0.09	0.18 ± 0.08	1.2:1	43 ± 1
Koeleria cristata	40 ± 3.1	9 ± 1.2	0.20 ± 0.03	0.06 ± 0.01	3.3:1	38 ± 2
Group mean	36.7 ± 4.2	11.3 ± 2.1	0.31 ± 0.2	0.11 ± 0.1	2.8:1	40.7 ± 2.5
			August			
Agropyron spicatum	36 ± 3.0	7 ± 2.0	0.41 ± 0.05	0.06 ± 0.01	6.8:1	36 ± 2
Festuca idahoensis	34 ± 1.1	12 ± 2.9	0.48 ± 0.01	0.16 ± 0.04	3.0:1	42 ± 3
Koeleria cristata	47 ± 1.2	3 ± 0.2	0.17 ± 0.03	0.06 ± 0.01	2.8:1	8 ± 2
Group mean	39.0 ± 7.0	7.3 ± 4.5	0.35 ± 0.2	0.09 ± 0.1	3.9:1	28.7 ± 18.2

TABLE 4. Average (± S.D.) monthly percent nutrient and moisture content of forb species exhibiting the highest frequency of occurrence at Rush Point, River of No Return Wilderness, 1977–1978.

Species	Crude fiber	Crude protein	Ca	P	Ca:P	Moisture
			June			
Achillea millefolium	29 ± 6.0	16 ± 1.4	0.96 ± 0.21	0.25 ± 0.07	3.8:1	70 ± 2
Balsamorhiza saggittata	29 ± 2.1	20 ± 3.2	2.45 ± 1.15	0.26 ± 0.06	9.4:1	81 ± 3
Eriogonum umbellatum	27 ± 0.4	16 ± 3.9	0.79 ± 0.32	0.22 ± 0.07	3.6:1	66 ± 5
Frasera montana	22 ± 6.3	17 ± 0.3	0.42 ± 0.01	0.16 ± 0.01	2.6:1	78 ± 2
Hieracium albertinum	25 ± 1.5	18 ± 0.3	0.45 ± 0.29	0.22 ± 0.01	2.1:1	77 ± 3
Lithospermum ruderale	34 ± 4.9	19 ± 2.3	1.71 ± 0.67	0.19 ± 0.004	9.0:1	73 ± 2
Lupinus sericeus	24 ± 2.0	19 ± 1.3	1.58 ± 0.15	0.35 ± 0.01	4.5:1	74 ± 4
MEAN (± S.D.)	27.1 ± 3.9	17.9 ± 1.6	1.19 ± 0.8	0.24 ± 0.1	4.9:1	74.1 ± 5.1
			July			
Achillea millefolium	30 ± 1.8	14 ± 0.6	0.76 ± 0.47	0.23 ± 0.07	3.3:1	60 ± 2
Balsamorhiza saggittata	31 ± 6.4	14 ± 1.0	1.57 ± 0.83	0.21 ± 0.11	7.5:1	63 ± 3
Eriogonum umbellatum	27 ± 0.7	13 ± 2.4	1.66 ± 1.29	0.15 ± 0.05	11.1:1	56 ± 1
Frasera montana	27 ± 0.8	13 ± 0.7	1.11 ± 0.76	0.17 ± 0.06	6.5:1	60 ± 4
Hieracium albertinum	27 ± 4.4	11 ± 1.2	1.08 ± 0.29	0.20 ± 0.04	5.4:1	63 ± 2
Lithospermum ruderale	30 ± 0.4	14 ± 1.7	1.95 ± 2.04	0.25 ± 0.07	7.8:1	57 ± 2
Lupinus sericeus	26 ± 1.5	17 ± 1.0	1.09 ± 0.82	0.21 ± 0.02	5.2:1	62 ± 3
MEAN	28.3 ± 1.9	13.7 ± 1.8	1.32 ± 0.4	0.2 ± 0.03	6.6:1	60.1 ± 2.8
			August			
Achillea millefolium	31 ± 0.85	12 ± 2.3	1.13 ± 0.10	0.20 ± 0.02	5.7:1	53 ± 2
Balsamorhiza saggittata	29 ± 3.4	10 ± 1.8	1.48 ± 0.76	0.19 ± 0.03	7.8:1	52 ± 2
Eriogonum umbellatum	31 ± 1.4	8 ± 0.9	0.87 ± 0.04	0.15 ± 0.02	5.8:1	43 ± 3
Frasera montana	28 ± 0.7	8 ± 0.4	0.36 ± 0.08	0.10 ± 0.02	3.6:1	38 ± 1
Hieracium albertinum	32 ± 4.6	8 ± 2.6	1.10 ± 0.14	0.13 ± 0.01	8.5:1	57 ± 3
Lithospermum ruderale	30 ± 1.4	9 ± 0.6	2.03 ± 1.65	0.16 ± 0.08	12.7:1	49 ± 2
Lupinus sericeus	35 ± 1.2	8 ± 1.1	0.97 ± 0.05	0.12 ± 0.02	8.1:1	59 ± 3
MEAN	30.9 ± 2.3	9.0 ± 1.5	1.1 ± 0.5	0.15 ± 0.04	7.5:1	50.1 ± 7.5

adjust foraging strategies to seasonal changes in the quality of food resources.

Even in wilderness areas it is important to understand the nutritional and dietary planes of native herbivores. Management strategies such as prescribed and wild fires, using natural meadows as camp sites and aircraft landing sites, and seasonal hunting of big game all involve decisions that can benefit from the nutritional evaluation of vegetation and dietary strategies of resident wild ungulates. More data of this nature as well as further studies on population dynamics and behavior of resident herbivores will contribute to the essential understanding of the relatively pristine ecosystem included within the River of No Return Wilderness Area.

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LITERATURE CITED

ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1970. Official methods of analysis. 11th ed. Washington, D.C. 1015 pp.

Claar, J. J. 1973. Correlations of ungulate food habits and winter range conditions in the Idaho Primitive Area. Unpublished thesis. Univ. of Idaho, Moscow. 85 pp.

Cook, C. W., and L. E. Harris. 1968. Nutritive value of seasonal ranges. Utah. Agric. Expt. Sta. Bull. 472. 55 pp.

Hayden-Wing, L. D. 1980. Elk use of mountain meadows in the Idaho Primitive Area. Pages 40–46 *in* M. S. Boyce and L. D. Hayden-Wing, eds., North American elk: ecology, behavior and management. Univ. of Wyoming, Laramie. 294 pp.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and deer in the Idaho Primitive Area. Wildlife Monogr. 21:1–39.

Jaccard, P. 1912. The distribution of the flora of the alpine zone. New Phytologist 11:37–50.

Maynard, L. A., J. K. Loosli, H. F. Hintz, and R. G. Warner. 1979. Animal nutrition. McGraw-Hill Book Co., New York. 602 pp.

Middleton, G., and R. E. Stucky. 1954. The preparation of biological material for the determination of trace metals. Part I: A critical review of existing procedures. Analyst 78:532–542.

Mueggler, W. F., and C. A. Harris. 1969. Some vegetation and soil characteristics of mountain grasslands in central Idaho. Ecology 50:671–678.

National Research Council. 1975. Nutrient requirements of domestic animals. No. 5. Nutrient requirements of sheep. 5th rev. ed. Nat. Acad. Sci., Washington, D.C. 72 pp.

______. 1976. Nutrient requirements of domestic animals. No. 4. Nutrient requirements of beef cattle. 5th rev. ed. Nat. Acad. Sci., Washington, D.C. 56 pp.

Papageorgiou, N. K. 1978. Food preferences, feed intake, and protein requirements of red deer in central Greece. J. Wildlife Manage. 42:940–943.

Pederson, J. C., and K. T. Harper. 1978. Factors influencing productivity of two mule deer herds in Utah. J. Range Manage. 31:105–110.

Skovlin, J. M. 1967. Fluctuations in forage quality on summer range in the Blue Mountains. U.S. Dept. Agric. Forest Service Res. Paper PNW-44. 20 pp.

Snider, C. C., and J. M. Asplund. 1974. In vitro digestibility of deer foods from the Missouri Ozarks. J. Wildlife Manage. 38:20–31.

Steel, R. G. D., and J. H. Torrie. 1980. Principles and procedures of statistics: a biometrical approach. McGraw-Hill Book Co., New York. 633 pp.

Subcommittee on Range Research Methods of the Agricultural Board. 1962. Basic problems and techniques in range research. Nat. Acad. Science–Nat. Res. Council, Washington, D.C. 341 pp.

Tadmor, N. H., A. Briegher, I. Noy-Meir, R. W. Benjamin, and E. Eyal. 1975. An evaluation of the calibrated weight-estimate methods for measuring production in annual vegetation. J. Range Manage. 28:65–69.

Thorne, E. T., R. E. Dean, and W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. J. Wildlife Manage. 40:330–335.

Van Soest, P. J. 1963. Use of detergent in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. J. Assoc. Official Agricultural Chemists 46:829–835.

Verme, L. J. 1963. Effects of nutrition on growth of white-tailed deer fawns. Trans. North Amer. Wildlife Conf. 38:431–442.

Wing, L. D. 1969. Ecology and herbivore use of five mountain meadows in the Idaho Primitive Area. Unpublished thesis. Univ. of Idaho, Moscow. 215 pp.

PRODUCER-CONSUMER BIOMASS IN MONTANE FORESTS ON THE ARIZONA MOGOLLON PLATEAU

Warren P. Clary[1], Peter F. Ffolliott[2], and Frederic R. Larson[3]

Abstract.— A substantially complete compilation of producer-consumer biomass was achieved for two montane forest reference stands on the Arizona Mogollon Plateau. This compilation, containing published and previously unpublished data, shows these ponderosa-pine-dominated stands to be near the lower end of the biomass range of commercial forest types. The two stands averaged approximately 75 metric tons/ha of plant biomass. Consumers made up less than 0.01 percent of the forest biomass. About 9/10 of the measured consumer biomass consisted of domestic and native ruminants.

Knowledge of biomass quantity and distribution is useful for conceptualizing biological conditions of an ecosystem, and is necessary for the study of primary and secondary production, nutrient cycling, hydrology, and fire. Information on biomass is limited for many vegetation types. Consumer data are particularly lacking in forested ecosystems where mammalian herbivores are relatively less important than in grassland ecosystems. Comparatively open forests, such as those of the southwestern ponderosa pine (*Pinus ponderosa*) ecosystem, represent an intermediate ecological position between dense humid forests and the more arid grasslands. Although large herbivores are not as obvious here as in the grasslands, their roles are significant.

Many different tree densities may occur within a forest ecosystem. Each density provides a different combination of biological components. As information is accumulated from a variety of forested conditions, more accurate judgements can be made concerning the impact of vegetation management on the amount of plant and animal life likely to be supported.

The purpose of this paper is to synthesize the current published and unpublished information on producer-consumer biomass from several representative situations within the montane forest ecosystem on the Arizona Mogollon Plateau. These values are compared to situations where the forest stand has undergone severe changes.

Description of Study Areas

The study areas, part of the Colorado Plateau physiographic province (Fenneman 1931), lie immediately north of the Mogollon Rim in central Arizona. The ponderosa pine ecosystem occurs at elevations between 1830 and 2590 m, although ponderosa pine is most strongly dominant between 2130 and 2380 m (Schubert 1974). It spans the altitudinal range of Merriam's Transition Zone (Merriam 1890, 1898).

Most of the information presented was obtained from the Beaver Creek watershed south of Flagstaff, Arizona (Brown et al. 1974) and from Stermer Ridge near Heber, Arizona (Ffolliott and Baker 1977). A summary of their mean characteristics follows:

	Beaver Creek	*Stermer Ridge*
Elevation	2250 m	2100 m
Precipitation	635 mm	533 mm
Temperature	7 C	9 C
Soil parent rock	basalt and volcanic cinders	Coconino sandstone
Typical soil texture	silty clay and silty clay loam	fine sandy loam
Timber basal area	26.4 m^2/ha	14.9 m^2/ha
Timber volume growth	2.8 m^3/ha/yr	2.5 m^3/ha/yr

Ponderosa pine was the major tree species on both areas. Woodland species such as Gambel oak (*Quercus gambelii*) and alligator juniper (*Juniperus deppeana*) were often present, and quaking aspen (*Populus tremuloides*) was occasionally found. The herbaceous layer was dominated by such graminoids as mutton bluegrass (*Poa fendleriana*), bottlebrush squirreltail (*Sitanion hystrix*), blue grama (*Bouteloua gracilis*), black dropseed (*Sporobolus interruptus*), and dryland sedge (*Carex geophila*). In some areas Arizona fescue (*Festuca arizonica*) and mountain muhly (*Muhlenbergia montana*) were prevalent. Typical forbs and half-shrubs were showy aster (*Aster commutatus*), showy goldeneye (*Viguiera multiflora*), western ragweed (*Ambrosia psilostachya*), and broom snakeweed (*Gutierrezia sarothrae*). The shrub layer was represented by Gambel oak sprouts and an occasional buckbrush ceanothus (*Ceanothus fendleri*) or New Mexico locust (*Robinia neomexicana*).

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The vertebrate animal biomass was dominated by ruminants. Cattle (*Bos taurus*), elk (*Cervus canadensis*), and deer (*Odocoileus hemionus*) were the primary species. Important smaller mammals included deer mouse (*Peromyscus maniculatus*), brush mouse (*P. boylei*), Mexican woodrat (*Neotoma mexicana*), cliff chipmunk (*Eutamias dorsalis*), gray-collared chipmunk (*E. cinereicollis*), golden-mantled ground squirrel (*Spermophilus lateralis*), Mexican vole (*Microtus mexicanus*), cottontail (*Sylvilagus nuttallii*), and Abert squirrel (*Sciurus aberti*). Reptiles included eastern fence lizard (*Sceloporus undulatus*) and tree lizard (*Urosarus ornatus*). The more common birds included common flicker (*Colaptes auratus*), Steller's jay (*Cyanocitta stelleri*), white-breasted nuthatch (*Sitta carolinensis*), pygmy nuthatch (*S. pygmaea*), Grace's warbler (*Dendroica graciae*), and gray-headed junco (*Junco caniceps*). Insects and other invertebrates were excluded from this study.

Supplemental information from other ponderosa-pine-dominated montane forest stands was obtained from the Rattle Burn area southwest of Flagstaff (Campbell et al. 1977), from several wildfire burns northwest of Flagstaff (Lowe et al. 1978), and from an earlier informational synthesis (Clary 1978).

Background and Procedures

The information presented was synthesized from source data collected from the late 1950s to the late 1970s. Some of the information has not been reported previously, but much has been obtained from reports and publications from the primary reference areas and supplemental study areas. The biomass estimates are most complete on the two reference areas. Therefore, information from these will be presented as base condition for forest stands on the Mogollon Plateau. Estimates of how the biomass quantity and composition changes as tree density decreases from either cutting or fire are based on information from supplemental areas.

Assumptions for this synthesis include:

1. The primary reference areas represent typical uneven-aged cut-over ponderosa pine stands.
2. Typical forest grazing practices are followed on the cattle allotments.
3. A livestock animal-unit represents 1121 kg/ha live weight.
4. Native consumer populations have uniform distribution of sex and age classes.

Information sources used to estimate biomass are shown in Tables 1 and 2. Only aboveground living biomass near growing

Table 1. Sources of producer biomass estimates for Beaver Creek and Stermer Ridge.

Woody plants
  Ponderosa pine
    —Individual stem equations from Gholz et al. (1979). (Data from Fort Valley Experimental Forest, Arizona).
    —Stand tables from Brown et al. (1974) and Ffolliott and Baker (1977).
  Gambel oak
    —Individual stem equations based on file data, Shrub Sciences Laboratory, Provo, Utah.
    —Stand tables from Brown et al. (1974) and Ffolliott and Baker (1977).
  Alligator juniper
    —Individual stem biomass based on data from Barger and Ffolliott (1972) and Miller et al. (1981), and equations from Gholz et al. (1979).
    —Stand tables from Brown et al. (1974) and Ffolliott and Baker (1977).
  Aspen
    —Individual stem equations from Peterson et al. (1970).
    —Stand table from Brown et al. (1974).
  Shrubs (including Gambel oak sprouts)
    —Field sample for current leaf and twig growth adjusted to total biomass based on Whittaker and Woodwell (1969) and Brown (1976).

Herbaceous plants
  —Data from Clary (1975) and Ffolliott and Baker (1977).

season end was calculated. Two trophic levels are presented—producers and consumers. Because no reliable carnivore information was found, no attempt was made to estimate biomass of carnivores. Also, because of a lack of insect information for the herbaceous layer, no insect biomass was estimated for modified forest conditions.

Table 2. Sources of consumer biomass estimates for Beaver Creek and Stermer Ridge.[1]

- Domestic
  - Cattle
    - —Biomass based on average animal-unit-month carrying capacities (Clary 1975) and from field sampling of fecal dropping densities.
- Native
  - Elk
    - —Animal-days from fecal group data of Neff (1972), Kruse (1972), Clary and Larson (1971), Ffolliott and Baker (1977), and Neff (pers. comm.).
    - —Live weight per animal from Murie (1951) and Quimby and Johnson (1951).
  - Deer
    - —Animal-days from fecal group data of Neff (1972), Kruse (1972), Ffolliott and Baker (1977), and Neff (pers. comm.).
    - —Live weight per animal adjusted from McCulloch (1962).
  - Tree squirrels
    - —Density estimates from David Patton (pers. comm.).
    - —Live weight per animal from Patton et al. (1976).
  - Rabbits
    - —Density estimates from fecal count data of Costa et al. (1976).
    - —Live weights per animal from field sampling.
  - Ground-dwelling rodents
    - —Beaver Creek biomass from Goodwin and Hungerford (1979).
    - —Stermer Ridge density estimates by field trapping with calculations according to Schnabel method (Overton and Davis 1969), and home range areas estimated from wildlife literature.
  - Birds
    - —Beaver Creek breeding bird densities and live weights from Szaro (1976).
    - —Age-class distribution from Wiens and Innis (1974).
    - —Stermer Ridge bird densities determined by strip census. Live weights from Carothers et al. (1973).
  - Reptiles
    - —Density estimates from strip census and calculation method of Hayne (1949).
    - —Live weight per animal from University of Arizona collection.
  - Insects
    - —Direct sampling of insect biomass (dry weight) per unit weight of conifer and hardwood foliage from Ronald Young (pers. comm.).

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[1] Live weight multiplied by 0.3 gives dry weight (Davis and Golley 1965).

Differences in biomass on the supplemental study areas (with and without reductions in overstory tree density) are expressed as percent change because of some differences among areas in manner of data collection.

Results in Reference Areas

Producer

Plant biomass on the two reference areas, Beaver Creek and Stermer Ridge, totaled 83,459 and 67,943 kg/ha, respectively (Table 3). Coniferous trees made up approximately 89 percent and hardwood trees approximately 11 percent of the producer biomass, and shrubs and herbaceous plants contributed only trace amounts. The conifer category consisted of 98 percent ponderosa pine and 2

Table 3. Producer-consumer biomass estimates.

Life form	Beaver Creek	Stermer Ridge
Plant	(kg/ha dry weight)	
Woody plants		
Trees, coniferous		
Foliage	5,638	3,733
Branches	18,272	15,015
Boles	48,125	43,785
Total	72,035	62,533
Trees, deciduous		
Foliage	432	202
Branches	2,159	1,012
Boles	8,639	4,049
Total	11,230	5,263
Shrubs		
Foliage and current twigs	18	19
Other	54	57
Total	72	76
Total	83,337	67,872
Herbaceous plants	122	71
Plant total	83,459	67,943
Animal		
Domestic		
Cattle	6.11	2.32
Native		
Elk and deer	.60	.39
Ground rodents and rabbits	.10	.03
Tree squirrels	.05	.02
Birds	.09	.04
Reptiles	.04	.02
Insects	.39	.24
Total	1.27	.74
Animal total	7.38	3.06

percent alligator juniper. The deciduous tree biomass was nearly all Gambel oak with only a trace of aspen. Woody tissues dominated. Tree boles constituted 69 percent and branches made up 24 percent of the total producer biomass. Only 7 percent of the late growing-season standing crop biomass was foliage, which is the primary food source for most of the consumer component of the forest.

These proportions vary in their comparability to other forest types. Conifer stands are often 3–5 percent foliage, 12–17 percent branches, and 78–85 percent boles (Grier et al. 1981, Whittaker and Niering 1975). Balsam fir (*Abies balsamea*) may be 23 percent foliage and only 59 percent boles (Post 1970). Hardwoods are generally 2–3 percent foliage, 18–34 percent branches, and 63–79 percent boles (Crow 1978, Post 1970, Ovington et al. 1963). Thus, the montane conifer-dominated Mogollan Plateau forests are similar to other conifer forests in their proportion of foliage, but similar to many hardwood forests in the proportion of branches and boles. A possible reason is that most southwestern ponderosa pine forests are rather open. This open characteristic may encourage the production of large branches, a trait typical of southwestern ponderosa pine (Pearson 1950).

The tree biomass in these reference stands averaged approximately 75 metric tons/ha. This value is toward the lower end of the range of 50–300 tons/ha for Rocky Mountain forests suggested by Weaver and Forcella (1977). The value appears reasonable because the ponderosa pine vegetation type normally occupies the lowest elevation and the lowest precipitation zone of the commercial forest types in the Southwest. However, in climax or near-climax ponderosa pine stands on the Santa Catalina Mountains near Tucson, Arizona, the total stand biomasses were 213–330 percent greater than the reference stands of this study (Whittaker and Niering 1975). These relatively mature climax stands had double the basal area per hectare of the Mogollon Plateau reference stands, and their average stem age of 93–150 years was probably much greater. Although the age structure of the reference stands was not determined, the large number of small stems (Brown et al. 1974, Ffolliott and Baker 1977) suggests that these stands, and indeed most cut-over southwestern ponderosa pine stands (Pearson 1950), would have a much younger average age and much less accumulation of biomass than the stands of Whittaker and Niering (1975). While the latter stands apparently represented specific situations (sampled by 0.1-ha plots), the reference stand data of this study represented the average situation across several hundred hectares of forest. It is likely, therefore, to be acceptably representative of cutover forests. In comparison to several forests in other areas, the reference stands contain biomass equivalent to 17 percent of a 180-year-old Pacific silver fir (*Abies amabilis*) stand in Oregon (Grier et al. 1981), about 73 percent of several Wisconsin hardwood forests (Crow 1978), and about 185 percent of a 26-year-old mountain maple stand (*Acer spicatum*) in New Brunswick (Post 1970).

Consumer

The producer biomass supported a comparatively small amount of consumer biomass (Fig. 1). The consumer biomass was approximately 3 to 7 kg/ha, or less than 0.01 percent of the total. Domestic herbivores, principally cattle, made up 86 percent of consumer biomass. The remainder was contributed by a variety of native species (Table 3).

Nearly three-quarters of the native vertebrate consumer biomass was contributed by the large mammalian herbivores—elk and deer. The categories of "birds" and "ground rodents and rabbits" each contributed about one-tenth of the native vertebrate biomass, although it should be noted that rabbits generally have very low populations in southwestern ponderosa pine forests (Costa et al. 1976). The remaining vertebrate biomass values were contributed by "tree squirrels" and "reptiles." The insect biomass exceeded all categories of native vertebrates except "elk and deer."

Examination of the consumer distribution suggests that a majority of the native vertebrate biomass and nearly all livestock biomass were supported by herbaceous plants, which contributed less than one-half percent

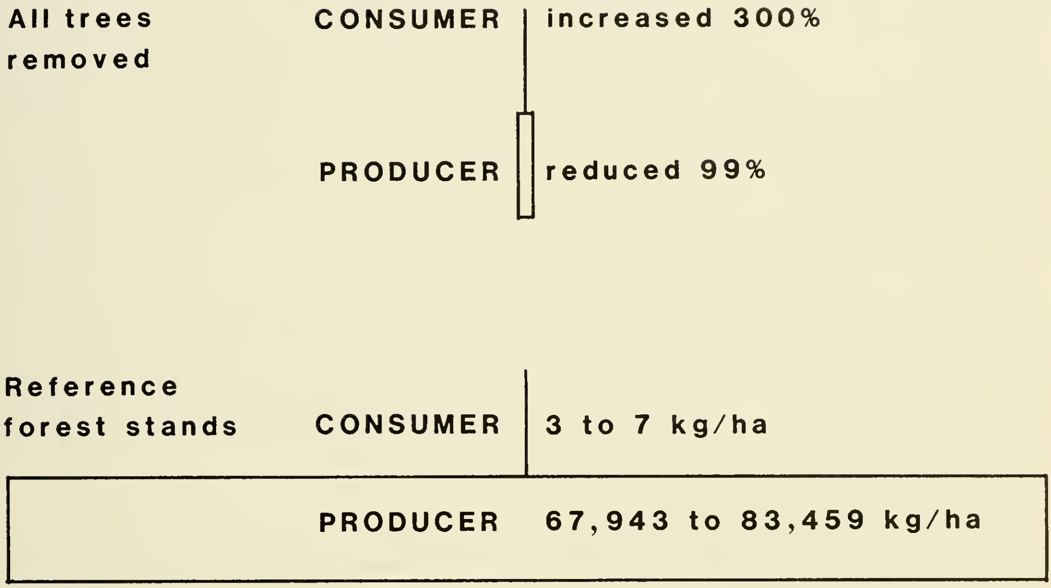

Fig. 1. Simplified biomass pyramid for reference stands, and the approximate proportional change following tree removal.

of the total biomass. Ponderosa pine trees appeared to provide the most direct food source and foraging substrate benefits to tree squirrels (Patton 1975), certain bird species (Szaro 1976), and certain insect species (Ronald Young, pers. comm.). Gambel oak foliage, which constitutes only about 6 percent of the woody plant foliage, apparently provides a substantial contribution to consumer nutrition. Oak leaves were a major component of mule deer summer diets on the Mogollon Plateau (Neff 1974), and Gambel oak foliage supported insect biomass at approximately five times the rate per unit weight of foliage as did ponderosa pine (Young, pers. comm.).

Normal activities of forest insects may be more important in energy flow and nutrient cycling than are other consumers. If consumption by insects approaches 7 percent of total forest foliage biomass (Whittaker and Woodwell 1969), insect consumption in these reference stands would approximate 350 kg/ha. This amount would greatly exceed that taken by all other consumers combined because it would exceed the total biomass of the shrub and herbage components. Insect consumption at only half this amount would still likely equal the amount taken by all other consumers.

The biomass values given represented late-growing season situations. Live biomass during midwinter would be lower. Nearly all of the herbage, all of the deciduous tree foliage, approximately one-third of the coniferous tree foliage, and a great majority of the consumer biomass would be absent then. The large herbivores, many birds, and some of the carnivores migrate to warmer winter habitats, leaving a much reduced consumer biomass.

The authors know of no other compilation of forest consumer biomass against which these reference stand estimates may be compared.

RESULTS IN AREAS AFTER REDUCTIONS IN TREE DENSITY

Several sources of information show what happened to the consumer biomass when partial reductions in the timber stand occurred (Table 4). As the forest density was reduced, tree foliage and total biomass were reduced, and the biomass of herbaceous and some shrubby plants increased. A parallel response in vertebrates occurred, with ground-feeding consumers tending to increase, and those species most directly dependent upon the trees, such as tree squirrels, tending to decrease as forest density was reduced. Some reductions in tree density occurred without reductions in bird life (Szaro 1976). If reductions in tree density result in accumulations of slash, large proportional increases can occur in small mammal populations (Goodwin and Hungerford 1979).

Total removal of trees resulted in much less foliage per hectare. Nevertheless, the increased herbaceous foliage supported a several hundred percent increase in vertebrate consumer biomass (Table 4). This increase was primarily a reflection of the difference in carrying capacity for livestock, although biomasses of many species of wildlife also increased when herbaceous plants increased. Because the productivity of herbaceous vegetation was higher, many ground-dwelling wildlife species maintained higher biomasses in the absence of trees, particularly when cover was present (Goodwin and Hungerford 1979, Campbell et al. 1977, Reynolds 1962). However, considerable variation in the densities of both small and large herbivores occurred, apparently because of cover requirements. Variations in the size of the opening, topography, presence of woody plants, and the presence of slash and other low cover will result in differences in native herbivore densities. Available information suggests variations of ± 60 percent to 80 percent will occur. Animal species shifts also occur as openings become large if little cover is present (pronghorn replace elk and deer, for example) (Clary 1978).

Tree squirrels and many birds were usually supported in higher biomasses in the forest than in the openings (Patton 1975, Szaro 1976). However, total bird biomass sometimes actually increases following tree removal when smaller tree-foraging birds are sufficiently replaced by larger ground-foraging species (Lowe et al. 1978). Different responses by birds to areas with trees removed were probably due to differing residual habitats. Little habitat variety remained after complete logging, whereas wildfire left a large number of standing dead trees that provided specialized habits for certain bird and small mammal species.

CONCLUSIONS

The ponderosa-pine-dominated reference stands on the Mogollon Plateau averaged approximately 75 metric tons/ha of plant biomass. Consumers made up less than 0.01 percent of the total forest biomass, but increased in stands where tree densities were reduced. However, even the loss of all trees resulted in a gain of only 20 to 30 kg/ha of consumer biomass.

These montane forests are near the lower end of the biomass range for commercial forest types, but we know of no forested situation for which equivalent estimates of consumer biomass are available. Therefore, no

TABLE 4. Percentage estimates of several biomass responses to reduction in forest stand densities.

	Percentages				
	Several ages of thinning[1]	Recent wildfire burn[2]	Recent wildfire burn[2]	Several ages of wildfire burn[3]	Several ages of logging[1]
Woody plants	29 decrease	44 decrease[5]	94 decrease[5]	99 decrease	100 decrease
Herbaceous plants	57 increase	128 increase	195 increase	270 increase	451 increase
Domestic animals					
Cattle	51 increase	14 increase	145 increase	–	375 increase
Native animals					
Elk and deer[6]	67 increase	125 increase	90 increase	105 increase	200 increase
Ground dwelling rodents	100 increase	109 increase	65 increase	40 increase	200 increase
Tree squirrels	50 decrease	–	–	–	100 decrease
Birds	no change	–	–	73 increase	90 decrease
Insects	–	–	–	–	–

[1] Clary 1978

[2] Campbell et al. 1977.

[3] Lowe et al. 1978.

[4] Basal area change.

Commercial volume change.

[6] Biomass of these larger animals is not supported on a continuous basis in forest openings because of their movements in and out. The biomass value given is proportional to the amount of use received.

comparisons are possible for the ability of the Mogollon Plateau forests to support consumer biomass in relation to other forest types. We do know that, because most of the vertebrate consumer biomass consisted of ruminant grazers, the secondary production in this forest is easily channeled into meat supplies for people.

We feel there should be more thorough investigations of biomass components of most biological systems. This would provide an improved basis for the understanding of the basic structure and functioning of natural and modified ecosystems.

Literature Cited

Barger, R. L., and P. F. Ffolliott. 1972. The physical characteristics and utilization of major woodland tree species in Arizona. USDA For. Serv. Res. Pap. RM-83. 80 pp.

Brown, H. E., M. B. Baker, Jr., J. J. Rogers, W. P. Clary, J. L. Kovner, F. R. Larson, C. C. Avery, and R. E. Campbell. 1974. Opportunities for increasing water yields and other multiple use values in ponderosa pine forest lands. USDA For. Serv. Res. Pap. RM-129. 36 pp.

Brown, J. K. 1976. Estimating shrub biomass from basal stem diameters. Canadian J. For. Res. 6:153–158.

Campbell, R. E., M. B. Baker, Jr., P. F. Ffolliott, F. R. Larson, and C. C. Avery. 1977. Wildfire effects on a ponderosa pine ecosystem: an Arizona case study. USDA For. Serv. Res. Pap. RM-191. 12 pp.

Carothers, S. W., J. R. Haldeman, and R. P. Balda. 1973. Breeding birds of the San Francisco Mountain area and the White Mountains, Arizona. Museum of Northern Arizona Tech. Ser. 12. Northern Arizona Society of Science and Art, Flagstaff. 54 pp.

Clary, W. P. 1975. Range management and its ecological basis in the ponderosa pine type of Arizona: the status of our knowledge. USDA For. Serv. Res. Pap. RM-158. 35 pp.

______. 1978. Producer-consumer biomass in Arizona ponderosa pine. USDA For. Serv. Gen. Tech. Rep. RM-56. 4 pp.

Clary, W. P., and F. R. Larson. 1971. Elk and deer use are related to food sources in Arizona ponderosa pine. USDA For. Serv. Res. Note RM-202. 4 pp.

Costa, R., P. F. Ffolliott, and D. R. Patton. 1976. Cottontail responses to forest management in southwestern ponderosa pine. USDA For. Serv. Res. Note RM-330. 4 pp.

Crow, T. R. 1978. Biomass and production in three contiguous forests in northern Wisconsin. Ecology 59:265–273.

Davis, D. E., and F. B. Golley. 1965. Principles in mammalogy. Van Nostrand Reinhold Co., New York. 335 pp.

Fenneman, N. M. 1931. Physiography of western United States. McGraw-Hill Book Co., Inc., New York. 534 pp.

Ffolliott, P. F., and M. B. Baker, Jr. 1977. Characteristics of Arizona ponderosa pine stands on sandstone soils. USDA For. Serv. Gen. Tech. Rep. RM-44. 7 pp.

Gholz, H. L., C. C. Grier, A. G. Campbell, and A. T. Brown. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Forest Research Laboratory, Oregon State University, Corvallis. Res. Pap. 41. 37 pp.

Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities and food habits in Arizona ponderosa pine forests. USDA For. Serv. Res. Pap. RM-214. 12 pp.

Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Canadian J. For. Res. 11:155–167.

Hayne, D. W. 1949. An examination of the strip census method for estimating animal populations. J. Wildl. Manage. 13:145–157.

Kruse, W. H. 1972. Effects of wildfire on elk and deer use of a ponderosa pine forest. USDA For. Serv. Res. Note RM-226. 4 pp.

Lowe, P. O., P. F. Ffolliott, J. H. Dieterich, and D. R. Patton. 1978. Determining potential wildlife benefits from wildfire in Arizona ponderosa pine forests. USDA For. Serv. Gen. Tech. Rep. RM-52. 12 pp.

McCulloch, C. Y. 1962. Influence on carrying capacity of experimental water conservation measures. Ariz. FAP W78 R-6; WP5, J7. Ariz. Game and Fish Dept., Phoeniz, Arizona. 19 pp.

Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado in Arizona. USDA, Div. of Ornithology and Mammalogy, North American Fauna 3. 136 pp.

______. 1898. Life zones and crop zones of the United States. USDA, Div. of Biological Survey Bull. 10. 79 pp.

Miller, E. L., R. O. Meeuwig, and J. D. Budy. 1981. Biomass of singleleaf pinyon and Utah juniper. USDA Forest Serv. Res. Pap. INT-273. 18 pp.

Murie, O. J. 1951. The elk of North America. Stockpole and Co., Harrisburg, Pennsylvania, and the Wildl. Manage. Inst., Washington, D.C. 376 pp.

Neff, D. J. 1972. Responses of deer and elk to Beaver Creek watershed treatments. Annu. Ariz. Watershed Symp. Proc. 16:18–24.

______. 1974. Forage preferences of trained mule deer on the Beaver Creek watersheds. Ariz. Game and Fish Dept. Spec. Rep. 4. 61 pp.

Overton, W. S., and D. E. Davis. 1969. Estimating the numbers of animals in wildlife populations. Pages 403–456 *in* Robert H. Giles, Jr., ed., Wildlife management techniques. Wildlife Society. 623 pp.

Ovington, J. D., D. Heitkamp, and D. B. Lawrence. 1963. Plant biomass and productivity of prairie, savanna, oakwood, and maize field ecosystems in central Minnesota. Ecology 44:52–63.

Patton, D. R. 1975. Abert squirrel cover requirements in southwestern ponderosa pine. USDA For. Serv. Res. Pap. RM-145. 12 pp.

Patton, D. R., T. D. Ratcliff, and K. J. Rogers. 1976. Weight and temperature of the Abert and Kaibab squirrels. Southwest. Nat. 21:236–238 .

Pearson, G. A. 1950. Management of ponderosa pine in the Southwest. USDA Monogr. 6. 218 pp.

Peterson, E. B., Y. H. Chan, and J. B. Cragg. 1970. Aboveground standing crop, leaf area, and caloric value in an aspen clone near Calgary, Alberta. Can. J. Bot. 48:1459–1469.

Post, L. J. 1970. Dry-matter production of mountain maple and balsam fir in northwestern New Brunswick. Ecology 51:548–550.

Quimby, D. C., and D. E. Johnson. 1951. Weights and measurements of Rocky Mountain elk. J. Wildl. Manage. 15:57–62.

Reynolds, H. G. 1962. Use of natural openings in a ponderosa pine forest of Arizona by deer, elk, and cattle. USDA For. Serv. Rocky Mt. For. and Range Exp. Stn. Res. Note 78. 4 pp.

Schubert, G. H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. USDA For. Serv. Res. Pap. RM-123. 71 pp.

Szaro, R. C. 1976. Population densities, habitat selection and foliage use by the birds of selected ponderosa pine forest areas in the Beaver Creek watershed, Arizona. Unpublished dissertation. Northern Arizona Univ., Flagstaff. 378 pp.

Weaver, T., and F. Forcella. 1977. Biomass of fifty conifer forests and nutrient exports associated with their harvest. Great Basin Nat. 37:395–401.

Weins, J. A., and G. S. Innis. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. Ecology 55:730–746.

Whittaker, R. H., and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. Ecology 56:771–790.

Whittaker, R. H., and G. M. Woodwell. 1969. Structure, production, and diversity of the oak-pine forest at Brookhaven, New York. J. Ecol. 57:155–174.

ROLE OF LIVESTOCK AND BLACK-TAILED JACKRABBITS IN CHANGING ABUNDANCE OF *KOCHIA AMERICANA*[1]

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Abstract.— Historical accounts and matched photographs indicate sharp decline of once-abundant *Kochia americana* in eastern Great Basin vegetation since the early 1900s, most of the decline by the late 1950s. Exclosure data show further decline from 1957 to 1973, then some increase between 1970 and 1973 and 1976 and 1981. Utah sheep numbers, at maximum from 1925 to 1940 and declining steadily to the 1970s, may have induced the long-term changes. Black-tailed jackrabbits (*Lepus californicus*), could not have induced vegetation decline, but could have added to livestock pressure and abetted the trend. In 1972, rabbits near a cyclic high were indirectly estimated to completely utilize *K. americana* in Curlew Valley, northwestern Utah. In 1976–1977 at rabbit low, direct measurements show 4%–18% of plants browsed by late summer, about 30%–50% of herbage removed from browsed plants. The latter rose to 45%–82% by end of winter. Late-summer percent browsed may have risen slightly (11%–21%) in 1980–1981 at next rabbit high. Increase in *K. americana* density from 1973 to 1976, then a slight decrease from 1976 to 1980, suggests fluctuating *K. americana* abundance induced by rabbit browsing, superimposed on long-term *K. americana* decline and recovery.

This paper presents data on the degree to which black-tailed jackrabbits (*Lepus californicus*) utilize the chenopodiaceous half-shrub *Kochia americana* in the salt-desert shrub vegetation of western Utah and explores the role of jackrabbits and livestock in the historic changes of abundance reported for this species. Variously called "white sage" (Kearny et al. 1914), "brown sage" (Esplin et al. 1937), "grey molly" (Stewart et al. 1940), and "desert molly" (Cook 1961) by earlier authors and generally referred to as *Kochia vestita*, this halophytic suffrutescent half-shrub typically reaches heights of 5–20 cm. Its unbranched, vertical stems lignify and die each fall to be replaced by new spring growth rising from the root crown.

Kochia americana and other species of similar stature form a mosaic of vegetation types in the glacial Lake Bonneville basin, the patchwork of simple or monotypic communities reflecting variations in microtopography, salinity, and other soil variables. Historically, the species grew in extensive, nearly monotypic stands interdigitating with big sagebrush (*Artemisia tridentata*) at slightly higher elevations and merging with shadscale (*Atriplex confertifolia*) at its lower edge (Kearney et al. 1914). Alternatively, it grew and continues today as a co-dominant with shadscale, or with greasewood (*Sarcobatus vermiculatus*) at still lower elevations.

The species has moderate forage value for sheep (Esplin et al. 1937, Cook and Stoddart 1953, Clarke and West 1969) and is preferred by black-tailed jackrabbits (Clark 1979, 1981, Westoby 1980). Several observers (e.g., Cook 1961, Rogers 1980) have reported sharp declines in *K. americana* abundance and distribution between the early 1900s and the 1950–1970s. These declines may be part of the more general, grazing-induced vegetation changes occurring over this same period (Kearny et al. 1914, Christensen and Johnson 1964, Holmgren and Hutchings 1972, Rogers 1980). More recently, our own observations indicate some increase in *K. americana* in the past decade or so. This paper addresses this history of changes in *K. americana* and possible herbivorous causation.

Methods

Study Area

Measurements of *K. americana* density and biomass, utilization rates by jackrabbits, censuses of jackrabbits, and certain earlier studies to which we will refer were carried out in the Utah portion of 3300 km² Curlew Valley. The valley lies north of the Great Salt Lake in northwestern Utah and southern Idaho. Valley floor elevations range from 1585 to 1280 m, sloping toward the lake. A few isolated hills (maximum elevation ca 1585 m) occur in the study area. The climate, characteristic of the Great Basin Desert, has annual precipitation ranging from 180 to 420 mm, mostly as winter snow. Mean monthly temperatures range from -7 C in January to 23 C in July. Four major vegetation zones occur along the elevational gradient, including those dominated by Utah juniper (*Juniperus osteosperma*), big sagebrush, shadscale, and greasewood.

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Although in earlier years *K. americana* occurred in a mosaic of pure stands and sagebrush patches in Curlew Valley (Cook 1961), it is found largely in association with shadscale and greasewood today. In the shadscale type, *K. americana* occurs as scattered individuals and as a near co-dominant with shadscale. In greasewood, it reaches its largest form, often under the greasewood canopy, but also scattered in the interspaces between the dominant shrubs. Both vegetation types include variable amounts of squirreltail grass (*Sitanion hystrix*), halogeton (*Halogeton glomeratus*), peppergrass (*Lepidium perfoliatum*), and tansy-mustard (*Descuraina* spp.).

Vegetation Measurements

In April 1976 two 1-ha livestock-proof reference areas were established in the valley to measure jackrabbit use of *K. americana*, one in the shadscale type, one in greasewood. Corners of 24 2 × 8 m plots were randomly located within each enclosure.

Kochia americana plants were sampled in these areas in June at approximate peak standing crop (Shinn et al. 1975) in 1976–1977, in August or September in these years plus 1980, and in February 1977 and 1978. Two measures of jackrabbit use were taken. The first, "percent removal," was the percentage of standing crop removed from *K. americana* plants that had been browsed. Jackrabbits waste much of the plants on which they browse (Currie and Goodwin 1966, Shoemaker et al. 1976). Cut stems and wasted material around the base of plants are cues to browsing. Hence, percent removal includes both the amounts ingested and wasted.

Both plant biomass and percent removal were estimated on individual plants within plots by ocular calibration (Tadmor et al. 1975). Calibration trials were conducted each morning before data collection, and biomass and percent removed were visually estimated within the reference areas (Clark 1979).

Black-tailed jackrabbits are the only *Lepus* species in the lower elevations of Curlew Valley; although two cottontail species (*Sylvilagus nuttalli* and *Brachylagus idahoensis*) occur, they are scarce and restricted to habitats unlike the reference areas. Johnson (1961) surveyed food habits of rodents in similar Idaho rangeland and found that none ate significant amounts of *K. americana*, although it occurred in his study area. Hence, the observed browsing probably was nearly all by jackrabbits.

The second measure of jackrabbit use in the reference areas was the percentage of all *K. americana* plants within plots showing some utilization (Stoddart et al. 1975) and is hereinafter called "percent browsed." During the same months these measurements were made in the reference areas, similar percent-browsed observations were made on 100 *K. americana* plants along each of a number of transects randomly located through the Utah portion of Curlew Valley. Transects also were sampled in July 1981. Observed plants were selected by the wandering quarter method (Catana 1963).

Kochia americana density was measured in the reference areas in 1976 and 1980 with the 24 plots/exclosure as described; in summer 1981 at an exclosure, originally livestock- and jackrabbit-proof, established in 1957 by E. H. Cronin in about the center of the Utah portion of Curlew Valley; and at an exclosure termed CO4 by Rice and Westoby (1978) in the western part of the valley. At the Cronin exclosure, we placed 8 transects with a total of 121 0.1-m² quadrats each inside and outside, 6 m from and parallel to the fence. At CO4, we established 4 transects with a total of 40 0.2-m² quadrats each inside and outside, similarly oriented to the fence.

Unless otherwise noted, all plant means reported are accompanied by one standard deviation. Probability levels for all statistical tests are the probability of a greater test statistic, assuming that the null hypothesis is true.

Jackrabbit Census

Jackrabbit populations in the Utah portion of Curlew Valley have been censused since fall 1962 as described in Gross et al. (1974). During the years of the present study, censuses were conducted by L. C. Stoddart (pers. comm.).

Results

Historical Changes in *K. americana* Abundance

Early 1900s to 1950s–1970s

To our knowledge, the abundance of *K. americana* in salt-desert shrub vegetation of the eastern Great Basin at the time of European settlement was not recorded and is not known. Early explorers and settlers apparently lumped all salt-desert shrubs and half-shrubs in the single category "sage" or "sagebrush" (Christensen and Johnson 1964). Thus, although early reports describe the altitudinal distribution of shrub zones, it is not possible to distinguish the species and their abundance and distribution.

Nevertheless, several important accounts were recorded by the early 1900s. Kearny et al. (1914) presented a map of extensive (several km^2), nearly monotypic *K. americana* zones in the vicinity of Tooele and Grantsville, Utah. Rogers (1980) reproduced photographs taken in 1912 in three areas of Tooele Valley showing similar monotypic stands. Cook (1961) inferred that such stands occurred in a mosaic with patches of sagebrush in Curlew Valley at some time preceding his observations in the late 1950s.

Kochia americana evidently declined in abundance between those early years and the decades of the 1950–1970s. Rogers (1980) photographed the original Shantz (Kearney et al. 1914) sites in Tooele Valley in 1978 and found former *K. americana* areas now occupied by exotic annuals and some weedy perennials (e.g., *Xanthocephalum sarothrae* and *Chrysothamnus nauseosus*). By the late 1950s, Cook (1961) found openings in sagebrush in Curlew Valley, which he inferred had previously been in *K. americana,* now largely covered with the exotic halogeton. Evidence of previous *K. americana* occupancy was provided by dead *K. americana* root crowns protruding from the soil surface. Similarly, in spring 1962, Dwayne Goodwin showed F. H. Wagner numerous dead root crowns in openings between sagebrush stands that were barren of live perennials. Thus, most of the decline probably occurred between early dates of abundance and the late 1950s.

Changes from 1950s to 1970s

Evidence of the past 24 years points to some further reduction during this period. When the Cronin exclosure was established in 1957, the *K. americana* density was comparable inside and outside the fence. In 1972, Westoby (1973) measured *K. americana* cover both inside and outside the exclosure and found it 25 times more abundant inside (0.25% vs. 0.01%). Today, a casual glance shows *K. americana* to be a common species inside the fence, but virtually nonexistent outside. In summer 1981 our measurements showed *K. americana* density at $3.5 \pm 9.9/m^2$ inside the same exclosure and $0.1 \pm 8.9/m^2$ outside (Table 1). Clearly *K. americana* has declined outside the exclosure in this area since 1957.

Table 1. Comparison of *K. americana* cover and density between 1972–73 and 1981 at two exclosures in Curlew Valley, Utah.

Exclosure and location	% cover ± std. dev. (N)		Plants/m^2 ± std. dev. (N)	
	1972[1]	1981[2]	1973[3]	1981[2]
Cronin inside	0.25	2.5 ± 6.6 (121)	–	3.5 ± 9.9 (121)
Cronin outside	0.01	0.04 ± 0.2 (121)	–	0.1 ± 8.9 (121)
CO4 inside	0.8	1.2 ± 2.7 (40)	2	4.7 ± 10.0 (40)
CO4 ouside	0.3	1.2 ± 2.3 (40)	2	4.0 ± 7.7 (40)

[1] From Westoby (1973)
[2] This study
[3] From Rice and Westoby (1978)

Changes from 1971 to 1981

Several lines of evidence suggest that *K. americana* abundance may have reached a low point in the early 1970s and recovered in the last decade. The first is a comparison of standing-crop biomass measured in 1972 in several areas of Curlew Valley by Westoby (1973) with our own more recent measurements in the two reference areas. We estimated dry weight per live plant in late summer 1976, 1977, and 1980 (Table 2). The grand mean of 7.1 g/plant is 11.8 times the 0.6 obtained by Westoby (unpubl. data). Combining the density (Table 3) and dry-weight data for each area yields estimates of 16.0 ± 21.0 g/m^2 in the shadscale area, 6.0 ± 38.7 g/m^2 for the greasewood area. These values, more than 11.8 times the yearly average standing crop of 0.2 g/m^2 measured by Westoby (1973) in 1972 for his studied portions of the valley, imply greater density of plants and considerably greater standing crop. He estimated 2.4 g/m^2 average standing crop at the same greasewood site as the reference area in this study where we measured 6.0 g/m^2.

Secondly, in summer 1981, we estimated *K. americana* density and cover in the Cronin exclosure and Exclosure CO4, both measured 8–9 years earlier. The comparative figures (Table 1) show definite increase in both areas. Although Westoby (1973) considered the Cronin exclosure to be jackrabbit-proof in 1972, the fence is now perforated in several places and the interior accessible to rabbits. In 1981, as in 1973 (Rice and Westoby 1978), the fence around CO4 was not jackrabbit-proof and the interior subject to their use. Both are livestock-proof.

Changes from 1976 to 1980

Kochia americana density measurements in 1976 and 1980 (Table 3) suggest some slight decline in the two reference areas during the four-year period ($F = 5.93$, $df = 1,68$; $P = 0.018$). Analysis of variance also showed the 2.6/m^2 in the greasewood area to be significantly greater than the 1.1/m^2 in the shadscale area ($F = 53.32$; $df = 1,68$; $P < 0.001$), although dry-weight/plant (Table 2) was significantly less in the greasewood zone ($F = 103.3$; $df = 1,2$; $P < 0.001$).

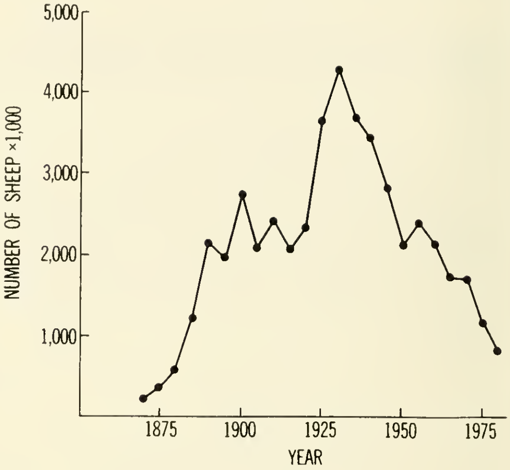

Fig. 1. Annual number of stock sheep plus lambs in Utah as reported by the USDA Statistical Reporting Service. Before 1924, only stock sheep were reported. Because the totals from 1925 to 1940 generally equaled 1.5–1.6 times the number of stock sheep, the latter values for 1870–1920 were multiplied by 1.5 to give the values in the graph.

Changes in Herbivore Numbers

Sheep

Because the value of *K. americana* to livestock generally is considered to be its use as winter sheep forage, only sheep numbers are considered here. USDA Statistical Reporting Service estimates of sheep numbers in Utah date back to 1870 and show a steady rise from low initial numbers to something over 2 million in 1890 (Fig. 1). They remained at

Table 2. Dry-weight biomass per live *K. americana* plant in two reference areas in Curlew Valley, Utah.

	Mean biomass, g/plant ± 1 std. dev. (N)		
Sampling period	Shadscale area	Greasewood area	Period means
September 1976	20.1 ± 35.1 (380)	2.3 ± 36.6 (931)	7.5 ± 36.2 (1311)
September 1977	8.4 ± 19.4 (311)	1.6 ± 20.1 (239)	5.4 ± 19.7 (550)
August 1980	12.8 ± 20.5 (151)	3.5 ± 8.7 (138)	8.4 ± 14.9 (289)
Area means	14.5 ± 26.7 (842)	2.3 ± 30.6 (1,308)	7.1 ± 19.1 (2,150)

about this level for the next 30 years, then rose to somewhere near 4 million between 1925 and 1940. Peak numbers were reached about 1930, and the industry declined thereafter. Numbers dropped below 1 million in the later 1970s, a level above which the industry had operated for nearly a century.

The records for Curlew Valley are not as complete, but Rice and Westoby (1978) have described several stages of livestock use in the valley that indicate declining grazing pressure from intensive use in 1869–1919 to the present. In this first half century, the area was a main travel route for herds driven to the railroad at its south end. This pressure disappeared in 1919 when the railroad was rerouted. Sheep and cattle grazing by local stockmen continued up to the present, but at declining levels, and today the grazing pressure probably is at the lowest level of a century or more. Present sheep grazing is confined to areas at least 15 km south of the locations where jackrabbit use of vegetation was estimated.

Jackrabbits

There has been a tendency in the small-mammal literature to consider black-tailed jackrabbits as seral animals that occur in greater numbers in disturbed areas (Vorhies and Taylor 1933, Phillips 1936, Smith 1940, Tiemeier 1965), although Flinders and Hansen's (1975) and MacCracken and Hansen's (1982) later findings do not follow the pattern. The tendency arising out of the earlier literature has been to assume that jackrabbits have increased since settlement as a result of grazing-induced vegetation changes (Taylor et al. 1935, Smith 1940, Taylor and Lay 1944).

Nevertheless, most of this theory comes from grassland (including desert grassland) regions. Jackrabbits evidently were quite abundant in the more arid West at settlement time and before. Early settlers in what is now Utah recounted as early as 1860 large numbers of jackrabbits, in some cases decimating cultivated crops and serving as a dietary staple for Indian inhabitants (Christensen and Johnson 1964, Christensen and Hutchinson 1965). Palmer (1897) compiled a number of reports, some for northern Utah and southern Idaho, of high jackrabbit populations as early as 1854. One is from E. T. Seton for the Curlew Valley area in 1888. A number of accounts suggest pronounced population fluctuations.

First population measurements in northern Utah were begun in 1951 by Woodbury (1955) when populations were thought to have been at a cyclic peak. They declined during the 1950s, then recovered to another in 1959 measured by French et al. (1965) in southern Idaho. This high occurred about 1960 in Curlew Valley (Currie and Goodwin 1966, Gross et al. 1974). Since then, jackrabbit populations have been censused annually in Curlew Valley, the approximate 10-year cycle peaking in 1970 and again in 1980 (Fig. 2).

The long-term trend on which this 10-year periodicity is superimposed can only be speculated on. Early accounts suggest densities greater than what we experience today (Christensen and Johnson 1964), and a long-term trend in abundance that is generally downward (French and Heasley 1981).

Subjectively, the 1970 high seemed to be lower than the 1959–1960 high to those of us who had witnessed both. And the censuses in Curlew Valley clearly show the 1980 peak to have been about twice that of 1970.

In total, early densities seem to have been high and may have declined somewhat in the present century, perhaps to a low point in the 1960s and 1970s. Whether or not the higher numbers of the 1979–1981 peak portend a reversal of the trend remains to be seen.

Table 3. Density of *K. americana* at two reference areas in Curlew Valley, Utah.

	Mean density, plants/m² ± std. dev. (N)		
Sampling period	Shadscale area	Greasewood area	Period means
May 1976	1.2 ± 0.9 (24)	2.8 ± 1.1 (24)	2.0 ± 1.0 (48)
August 1980	0.8 ± 0.4 (12)	2.1 ± 0.7 (12)	1.5 ± 0.6 (24)
Area means	1.1 ± 0.7 (36)	2.6 ± 1.0 (36)	1.8 ± 0.9 (72)

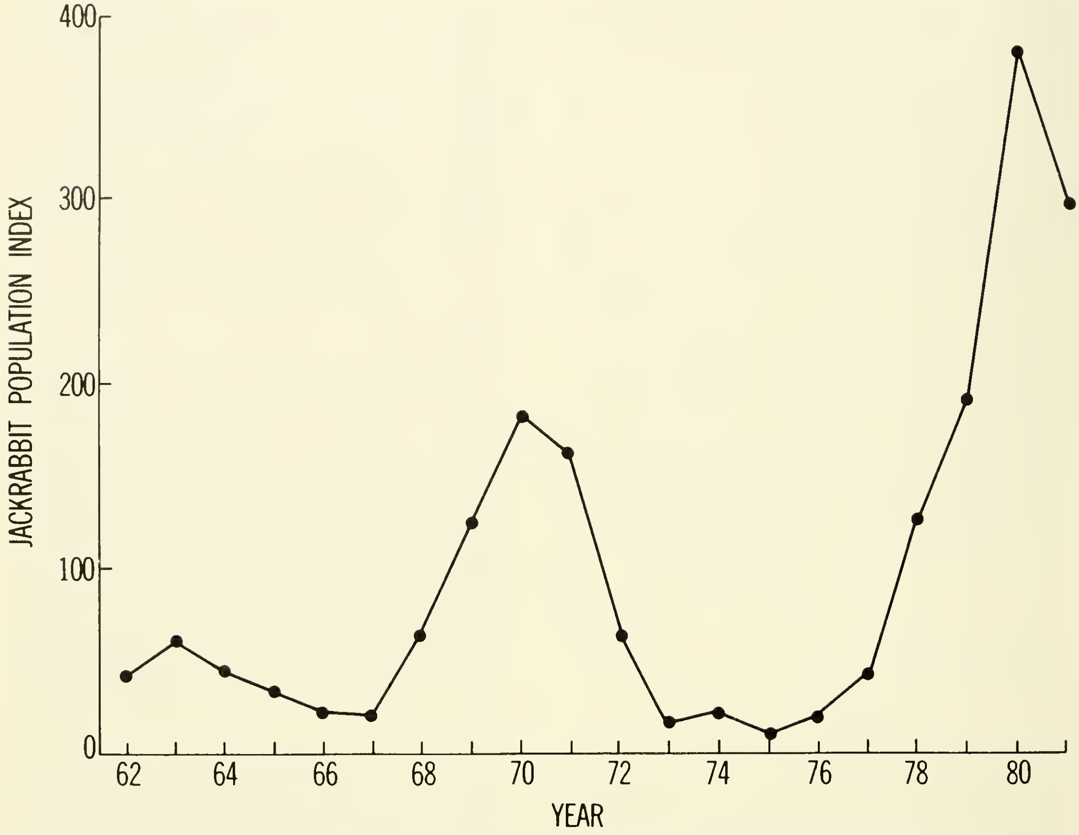

Fig. 2. Indices of black-tailed jackrabbit population density in Curlew Valley, northwestern Utah. Census method is described in Gross et al. (1974), and the data are from L. C. Stoddart (pers. comm.).

Jackrabbit Impacts on *K. americana*

Effects on Individual Plants

The percentage of aboveground phytomass removed from individual *K. americana* plants (Table 4) seems to increase progressively from early summer, at the time of peak standing crop, to midwinter. This is expected, both because the rabbit population increases during the summer from reproduction and because fewer foods are available in winter (Clark 1979), so rabbits browse for a longer time on a selected plant.

By the end of summer, when the plants were lignifying, rabbits had removed from 33% to 50% of the phytomass on browsed plants in the three years of observation. By February 1977 and 1978, two low rabbit years, these values had risen to somewhere between 45% and 82% by the end of winter.

Similarly, Currie and Goodwin (1966) noted that jackrabbits remove a large proportion of herbage from individual plants when

Table 4. Percentage of herbage removed by jackrabbits from individual *K. americana* plants on two reference areas in Curlew Valley, Utah.

	Mean % removed/ plant ± std. dev. (N)	
Sampling period	Shadscale area	Greasewood area
June 1976	10.9 ± 4.9 (6)	18.9 ± 6.6 (6)
September 1976	31.0 ± 17.8 (29)	47.2 ± 37.1 (164)
February 1977	64.9 ± 65.1 (49)	81.7 ± 11.1 (3)
June 1977	13.2 ± 2.7 (2)	11.0 ± - (1)
September 1977	42.2 ± 15.5 (13)	48.4 ± 11.7 (22)
February 1978	45.9 ± 19.5 (105)	45.6 ± 3.7 (8)
August 1980	37.7 ± 16.1 (22)	32.3 ± 15.8 (15)

they select one they prefer during a feeding period. Occasionally, they clip off small shrubs, such as *K. americana*, at ground level. In September 1981, *K. americana* plants were actually dug out of the ground, apparently to chew the root crown and cambium around the base of the stem. In 20 1-m^2 quadrats placed at 3-m intervals along a transect immediately west of the greasewood reference area, 11 of 93 plants (12%) had been dug out and partly eaten.

Mean percentage of herbage removed from plants in the greasewood area (46.2 ± 32.7%) in August–September of the three years (Table 4) was significantly greater than that (35.6 ± 16.7%) removed in the shadscale area ($F = 5.75$; $df = 1,2$; $P = 0.018$). This may have been due to the smaller stature of the plants in the greasewood area (Table 2).

We tested the null hypothesis that the August–September percentages for the three years were equal and found no significant differences ($F = 1.89$; $df = 2,2$; $P = 0.346$). As jackrabbit density increases, as occurred from 1976 to 1981 (Fig. 2), one might expect more intense browsing on individual plants of this preferred species, but that was not the case in these years. Although individual plants may be heavily used, jackrabbits often skip over adjacent plants seemingly similar to those browsed.

If any between-year variation occurred, it was inversely correlated with the annual variations in biomass/plant, although the yearly means shown in Table 2 were not statistically different ($F = 0.1$; $df = 2,2$; $P = 0.999$). Yearly variations in the dry weight of half-shrubs such as *K. americana* probably are related to variations in precipitation (West and Fareed 1973).

Percentage of Plants Browsed

Like the percent removal, the percentage of plants browsed appears to increase from June to February (Table 5). This trend is clear for the shadscale area in both years and for the valleywide transects in 1977–1978. In these areas, percent browsed rose from about 1%–3% in June to about 4%–8% in September of the low rabbit years 1976 and 1977, and to 8.4% by February of these same years. The progressive increase in percent browsed, also like percent removal, would be expected to be a cumulative parameter both as the rabbit population increased through the summer and as an increasing fraction of the plants were selected and fed upon.

In 1980 and 1981, at peak rabbit population, measured late-summer percentages in the shadscale and transect areas were 15%–21%. Because no winter measurements were made in these years, the final percentage of plants browsed before the next growing season was undoubtedly higher. Furthermore, the late-summer digging described probably increased further the percentage of plants affected by rabbits, unless for some reason (e.g., palatability) the digging was confined to already-browsed plants.

The percent browsed increased from June to September in the greasewood reference area, as in the other areas, but then declined from September to February. Inasmuch as measurements were restricted to freshly

Table 5. Percentage of *K. americana* plants browsed by jackrabbits on two reference areas and valleywide transects in Curlew Valley, Utah.

	Mean % browsed ± std. dev. (N)[1]		
Sampling period	Shadscale area	Greasewood area	Transects
June 1976	1.2 ± 0.4 (12)	1.1 ± 0.4 (24)	–
September 1976	7.6 ± 1.4 (24)	17.7 ± 1.3 (24)	–
February 1977	13.8 ± 1.8 (24)	1.0 ± 0.6 (24)	–
June 1977	0.7 ± 0.5 (24)	0.4 ± 0.4 (24)	3.1 ± 3.0 (14)
September 1977	4.2 ± 1.1 (24)	9.2 ± 1.9 (24)	5.8 ± 4.3 (12)
February 1978	38.6 ± 3.0 (24)	3.8 ± 1.9 (24)	7.9 ± 5.1 (7)
August 1980	14.6 ± 2.9 (12)	10.9 ± 2.7 (12)	15.3 ± 6.9 (10)
July 1981	–	–	21.4 ± 11.6 (12)

[1] No. of quadrats for reference areas, no. of transects valleywide

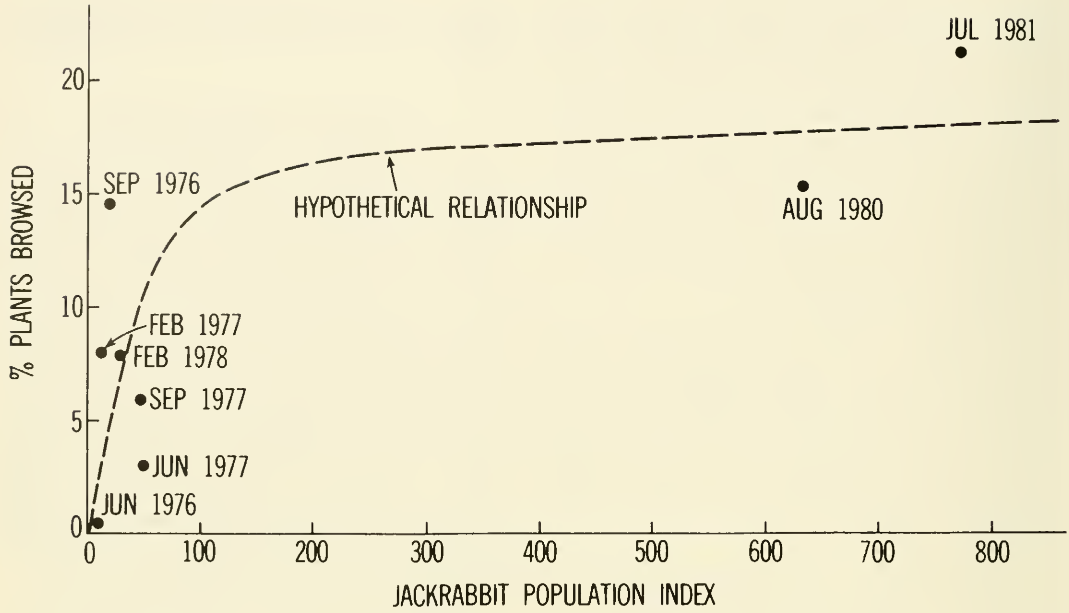

Fig. 3. Relationship between percentage of *K. americana* browsed by jackrabbits and jackrabbit population index in Curlew Valley, Utah. The points for 1976 are from the reference areas only; the remaining points are from transects throughout the valley.

browsed plants, the explanation probably lies in the high density (Table 3) of *K. americana* within the greasewood area. During 1976–1978, many small (<1.0 g/plant) *K. americana* plants sprouted from old root crowns in the spaces between the greasewood. These small plants were largely ignored by rabbits, especially in the winter when they were drier than larger, more robust plants. Because feeding by rabbits is patchy, varying with plant condition, plant density, and habitat, the transects that were located in a variety of areas probably are the best indicators of valleywide patterns.

To explore further the question of whether the percentage of plants browsed by jackrabbits increases as they increase, we tested the null hypothesis that the August–September percentages were the same at both reference areas between years (Table 5). We concluded that the percent browsed did differ significantly between years ($X^2 = 28.04$; $df = 3$; $P < 0.001$).

Because the reference areas are only a small part of Curlew Valley, we also tested, with data from the transects, the hypothesis that dense populations browse a larger percentage of the *K. americana* plants (Table 5). Mean percentage of plants browsed on transects in September 1977, August 1980, and July 1981 is significantly different when compared by a Kruskal-Wallis test ($X^2 = 14.64$; $df = 2$; $P = 0.001$; Sokal and Rohlf 1969:388–390). Thus, on the basis of evidence from both reference areas and transects, higher rabbit populations do affect more *K. americana* plants.

On the basis of empirical evidence, Clark (1979) predicted that if the relationship between *K. americana* use and jackrabbit density were linear, 90% of all *K. americana* plants would be browsed during the highest population periods. Westoby (1974), on the basis of more theoretical arguments, concluded that preferred, palatable, and rare plants such as *K. americana* would be under severe browsing pressure from rabbits. To test these predictions, we examined the relationship between percentage of plants browsed and the jackrabbit population index by using all occasions for which we had measurements of both variables (Fig. 3). Although the figure is sketchy, it suggests a curvilinear relationship, not a linear one. Even at the highest rabbit population levels recorded in two decades (Fig. 2), only about 20% of the plants were browsed by late summer. By regressing percent browsed (Y) on the logarithm of jackrabbit population index (X), we produced an adequate equation to predict what browsing levels would be under extremely high populations ($F = 6.69$; $df = 6$; $P = 0.04$; $r = 0.73$). $Y = -2.06 + 2.94X$.

At the highest population levels for which we had data on percent browsed, the relationship predicts mean utilization of about 17%, with 95% confidence limits of approximately 2%–33%. Because it is possible that historical rabbit population levels were much higher, we made a similar prediction for a population index of 1550, twice as abundant as our highest observed levels. Predicted mean percent browsed was only 20%, with 95% confidence limits of approximately 3%–36%. Even at the highest population levels, percent browsed by rabbits does not even approach 100% of the *K. americana* plants.

DISCUSSION AND CONCLUSIONS

Kochia americana was an abundant species in the salt-desert shrub vegetation of the eastern Great Basin in the early 1900s and, we suspect, as early as European settlement. The species declined sharply in this century in the areas of nearly pure stands, as shown by the photographic evidence and the dead root-crown remains seen as late as the early 1960s. Whether or not its density declined in those areas where it coexists with shadscale or greasewood is unknown. The evidence suggests an increase in *K. americana* abundance in these types since the early 1970s, much as it is increasing in the openings where it formerly occurred in pure stands.

Why the species declined so sharply is a matter of speculation, but we suspect that the primary stimulus was grazing livestock, primarily sheep. The view that livestock numbers built up to historically high numbers and that the major changes in range vegetation occurred before 1900 is encountered in the range literature. But sustained, maximum numbers of both sheep and cattle did not build up in the West until well into the 20th century (Wagner 1978).

In Utah, sheep numbers did not rise well above 2 million until 1900, and then they remained above this level for more than half a century (Fig. 1). Peak numbers were reached in about 1930. If the area under the curve in Fig. 1 is taken as the total sheep-grazing pressure on Utah ranges since settlement, then only about 16% was incurred from 1870 to 1900, whereas about 63% was applied from 1900 to 1950.

Black-tailed jackrabbits were abundant in Utah at settlement time, as was *K. americana*. Hence, its decline probably was not primarily induced by rabbit browsing, with which it had long coexisted. However, jackrabbit browsing may have added to the sheep pressure, providing a collective effect that was more than *K. americana* could sustain, and together they may have caused its shrinkage. Nevertheless, livestock was likely the major new variable that elicited the decline.

The hypothesis that livestock browsing, with or without jackrabbit pressure, was responsible for the decline in Curlew Valley, and not some other influence such as insects, disease, or weather, is supported by the exclosure data (Table 1). *Kochia americana* virtually disappeared outside the Cronin exclosure after 1957, but maintained a healthy stand inside. And, although the differences are not statistically significant, mean percent *K. americana* cover and density were greater inside Exclosure CO4 (established in 1956) than outside, both in Rice and Westoby's (1978) measurements in 1973 and ours in 1981.

A jackrabbit influence may be suggested by these results. The Cronin exclosure was jackrabbit-proof at least through 1972 (Westoby 1973). Jackrabbit protection in CO4 lapsed after 1969 (Rice and Westoby 1978). Perhaps significantly, the inside-outside difference is much more marked in the Cronin plot than in CO4 (Table 1).

The livestock influence may be inferred both from the *K. americana* decline during high sheep numbers and from the *K. americana* increase since the early 1970s, when sheep numbers have been profoundly reduced but jackrabbit grazing has continued. Parenthetically, the *K. americana* increase is contrary to Westoby's (1973, 1981) contention that the species could not recover because of salt deposition on the soil surface by halogeton.

The available data provide a closer look at the jackrabbit influence. Westoby (1973) concluded that *K. americana* was highly preferred by jackrabbits, whereas Clark (1979, 1981) found it only moderately preferred. Nevertheless, both investigators found the species a relatively minor dietary component.

At high rabbit density, and perhaps the low point of *K. americana* abundance in early 1972, Westoby calculated virtually complete utilization by the end of the year on the basis of known consumption rates, dietary composition, and estimated *K. americana* standing crop. Our own direct measurements of percent browsed show much lower rates in the low rabbit years of 1976 and 1977 (Table 5) and when *K. americana* evidently was more abundant than during Westoby's measurements. These are the expected results if *K. americana* has increased since the early 1970s: utilization rate is a positive function of the number of plants consumed per herbivore and the number of herbivores, and a negative function of the number of plants. Both a decrease in number of herbivores and an increase in the number of plants will tend to reduce the utilization rate.

Our measurements indicate somewhat higher late summer percentage of plants browsed in the high rabbit years of 1980 and 1981 (Table 5), although these are still lower than Westoby's estimate of total utilization. But, because his were calculated for year-long use and we did not make winter measurements in these two years, the two sets of rates may not be entirely comparable, nor can we say what the final, year-long utilization levels were in 1980 and 1981. Our data show 45%–82% removal of herbage from browsed plants by February of 1976 and 1977 (Table 4), both low rabbit years. We do not know what level of browsing an individual *K. americana* plant can sustain, although small plants can easily be destroyed by browsing jackrabbits. But even the percent removal of the low years, applied to an appreciable fraction of *K. americana* plants in high rabbit years, would seem to be a significant impact. If rabbit browsing during cyclic highs were intensive enough to kill an appreciable fraction of *K. americana* plants, this could produce variations in plant density. However, we can infer from our regression and the present abundance of *K. americana* that the year-long percentage of plants browsed has not reached 100%.

Collectively, the data suggest the following hypothetical scenario. *Kochia americana* was abundant in the salt-desert shrub vegetation of the eastern Great Basin up to the early 1900s in the presence of large jackrabbit populations, but under no, then initially moderate, livestock use. Between the early 1900s and the early 1970s it declined broadly, then appears to have increased in the 1970s and early 1980s. This general trend probably was induced by heavy livestock pressure in the first half of the century, then reduction of the pressure in the third quarter. The decline may have been abetted by jackrabbit browsing, but the recovery is occurring in the face of that browsing.

The sequence for Curlew Valley may have differed slightly because of its location as a livestock shipping route and the possibility of earlier livestock pressure. But, given the *K. americana* root crowns as late as 1962 and comparable density inside and outside Cronin's exclosure in 1957, its abundance evidently persisted well into the first half of this century.

Much more hypothetically, some short-term cyclic variation in *K. americana* abundance may be superimposed on the broad trend by cyclic jackrabbit pressure—at least in the middle of the century when *K. americana* was scarce in comparison with the early 1900s—and the ratio of jackrabbit herbivory to *K. americana* abundance may be higher than under pristine conditions. This hypothetical scenario needs to be tested with long-term, annual concurrent measurement of *K. americana* and jackrabbit densities.

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Literature Cited

Catana, A. J. 1963. The wandering quarter method of estimating population density. Ecology 44:349–360.

Christensen, E. M., and H. B. Johnson. 1964. Presettlement vegetation and vegetational change in three valleys of central Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 4(4). 16 pp.

Christensen, E. M., and M. A. Hutchinson. 1965. Historical observations on the ecology of Rush and Tooele valleys, Utah. Proc. Utah Acad. Sci., Arts, Lett. 42:90–105.

Clark, W. R. 1979. Population limitation of jackrabbits: an examination of the food hypothesis. Unpublished dissertation. Utah State Univ., Logan. 242 pp.

______. 1981. Role of black-tailed jackrabbits in a North American shrub-steppe ecosystem. Pages 706–719 *in* K. Myers and C. MacInnes, eds., Proceedings World Lagomorph Conference, Aug. 1979, Guelph, Ontario. 983 pp.

Clarke, L. D., and N. E. West. 1969. Germination of *Kochia americana* in relation to salinity. J. Range Manage. 22:286–287.

Cook, C. W. 1961. Seeding response and soil characteristics on adjacent sagebrush and desert molly soils. J. Range Manage. 14:134–138.

Cook, C. W., and L. A. Stoddart. 1953. The halogeton problem in Utah. Utah Agric. Exp. Sta. Bull. 364. 44 pp.

Currie, P. O., and D. W. Goodwin. 1966. Consumption of forage by black-tailed jackrabbits on salt-desert ranges of Utah. J. Wildl. Manage. 30:304–311.

Ellison, L. 1960. Influence of grazing in plant succession of rangelands. Bot. Rev. 26:2–66.

Esplin, A. C., J. E. Greaves, and L. A. Stoddart. 1937. A study of Utah's winter range: composition of forage plants and use of supplements. Utah Agric. Expt. Sta. Bull. 277. 48 pp.

Flinders, J. T., and R. M. Hansen. 1975. Spring population responses of cottontails and jackrabbits to cattle grazing shortgrass prairie. J. Range Manage. 28:290–293.

French, N. R., and J. E. Heasley. 1981. Lagomorphs in the shortgrass prairie. Pages 695–705 *in* K. Myers and C. MacInnes, eds., Proceedings World Lagomorph Conference, Aug. 1979, Guelph, Ontario. 983 pp.

French, N. R., R. McBride, and J. Detmer. 1965. Fertility and population density of the blacktail jackrabbit. J. Wildl. Manage. 29:14–26.

Gross, J. E., L. C. Stoddart, and F. H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. Wildl. Monogr. 40. 68 pp.

Holmgren, R. C., and S. S. Hutchings. 1972. Salt desert shrub response to grazing use. Pages 153–164 *in* C. M. McKell, J. P. Blaisdell, and J. R. Goodin, eds., Wildland shrubs—their biology and utilization. USDA For. Serv. Tech. Rep. INT-1. 494 pp.

Johnson, D. R. 1961. Food habits of rodents on rangelands of southern Idaho. Ecology 42:407–410.

Kearny, T. H., L. J. Briggs, H. L. Shantz, J. W. McLane, and R. L. Piemeisel. 1914. Indicator significance of vegetation in Tooele Valley, Utah. J. Agric. Res. 1:365–417, maps and photos.

MacCracken, J. G., and R. M. Hansen. 1982. Herbaceous vegetation of habitat used by blacktail jackrabbits and Nuttall cottontails in southeastern Idaho. Amer. Midl. Nat. 107:180–184.

Palmer, T. S. 1897. The jack rabbits of the United States. USDA Div. Biol. Surv. Bull. 8. 88 pp.

Phillips, P. 1936. The distribution of rodents in overgrazed and normal grasslands in central Oklahoma. Ecology 17:673–679.

Rice, B. L., and M. Westoby. 1978. Vegetation responses of some Great Basin shrub communities protected against jackrabbits or domestic stock. J. Range Manage. 31:28–34.

Rogers, G. F. 1980. Photographic documentation of vegetation changes in the Great Basin Desert. Unpublished dissertation. Univ. of Utah, Salt Lake City. 160 pp.

Shinn, R. S., R. D. Anderson, M. Merritt, W. Osborne, and J. A. MacMahon. 1975. Curlew Valley validation site report. USIBP Desert Biome Res. Memo. RM 75-1. Utah State Univ., Logan. 68 pp.

Shoemaker, V. H., K. A. Nagy, and W. R. Costa. 1976. Energy utilization and temperature regulation by jackrabbits (*Lepus californicus*) in the Mojave Desert. Physiol. Zool. 49:364–375.

Smith, C. C. 1940. The effect of overgrazing and erosion upon the biota of the mixed-grass prairie of Oklahoma. Ecology 21:381–397.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman Co., San Francisco. 776 pp.

Stewart, G., W. P. Cottam, and S. S. Hutchings. 1940. Influence of unrestricted grazing on northern salt desert plant associations in western Utah. J. Agric. Res. 60:289–316.

Stoddart, L. A., A. D. Smith, and T. W. Box. 1975. Range Management. 3d ed. McGraw-Hill Book Co., New York. 532 pp.

Tadmor, N. H., A. Brieghet, I. Noy-Meir, R. W. Benjamin, and E. Eyal. 1975. An evaluation of the weight-estimate method for measuring production in annual vegetation. J. Range Manage. 28:65–69.

Taylor, W. P., C. T. Vorhies, and P. B. Lister. 1935. The relation of jack rabbits to grazing in southern Arizona. J. For. 33:490–498.

Taylor, W. P., and D. W. Lay. 1944. Ecologic niches occupied by rabbits in eastern Texas. Ecology 25:120–121.

Tiemeier, O. W. 1965. Bionomics. Pages 5–37 *in* The black-tailed jackrabbit in Kansas. Kansas Agric. Expt. Sta. Tech. Bull. 140. 75 pp.

Vorhies, C. T., and W. P. Taylor. 1933. The life histories and ecology of jackrabbits, *Lepus alleni* and *Lepus californicus* spp., in relation to grazing in Arizona. Univ. Arizona Agric. Expt. Sta. Tech. Bull. 49. 117 pp.

Wagner, F. H. 1978. Livestock grazing and the livestock industry. Pages 121–145 *in* H. P. Brokaw, ed., Wildlife and America: contributions to an understanding of American wildlife and its conservation. U.S. Coun. Environ. Qual., U.S. Fish Wildl. Serv. U.S. For. Serv., U.S. Nat. Ocean. Atmos. Admin. 532 pp.

WEST, N. E., AND M. FAREED. 1973. Shoot growth and litter fall processes as they bear on primary production of some cool desert shrubs. USIBP Desert Biome Res. Memo. RM 73-9. Utah State Univ., Logan. 13 pp.

WESTOBY, M. 1973. Impact of black-tailed jackrabbits (*Lepus californicus*) on vegetation in Curlew Valley, northern Utah. Unpublished dissertation. Utah State Univ., Logan. 164 pp.

______. 1974. An analysis of diet selection by large generalist herbivores. Amer. Nat. 108:290–304.

______. 1980. Black-tailed jackrabbit diets in Curlew Valley, northern Utah. J. Wildl. Manage. 44:942–948.

______. 1981. Elements of a theory of vegetation dynamics in arid rangelands. Israel J. Bot. 28:169–194.

WOODBURY, A. M. 1955. Ecology of the Great Salt Lake desert. 1. An annual cycle of the jackrabbit. Ecology 36:353–356.

A PRELIMINARY CLASSIFICATION OF THE NATURAL VEGETATION OF COLORADO

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ABSTRACT.— A classification of the natural vegetation of Colorado is presented. This classification, which uses the Plant Association as the basic unit, was developed by sorting data in the scientific literature, supplemented by field research. The classification uses a standardized nomenclature. Citations are given for the literature from Colorado and adjoining states for each Association. The classification includes a total of 403 Plant Associations, with 28 Angiosperm Forests/Woodlands, 2 Mixed Angiosperm-Gymnosperm Forests/Woodlands, 114 Gymnosperm Forests/Woodlands, 100 Shrub Associations, 74 Grassland Associations, 38 Graminoid Associations, and 47 Herb Associations.

In completing a state flora, a species taxonomist (systematist) would compile existing collection records from herbaria, resolve pertinent taxonomic questions, adopt and synonymize nomenclature, and complete field collections in undercollected parts of the state. The syntaxonomist aiming at a state compilation of vegetation types would need to take analogous steps. In the western United States, however, there are additional problems specific to syntaxonomy: (1) There is no herbarium analog for vegetation records; the vegetation analog of a plant specimen is a sample (stand) record. Although these are often published in the scientific literature, in some states, such as Colorado, a substantial amount of stand data is not available in the published literature. (2) There is no single, widely utilized method of stand data collection. Stand attributes measured may include cover, frequency, biomass, percent composition, density, or other measures. These may be recorded for each species of plant, or plants may be grouped by life form or other criteria. Data may be collected using visual estimates on large plots, or by more detailed quadrat methods. (3) Many sample plot data are collected but never analyzed, or the analysis includes ordination but not classification. Although ordination procedures may assist in elucidating relationships among samples and in relation to environmental gradients, they are of less value than clustering procedures in determining meaningful vegetation units. (4) In the western U.S., with few exceptions, vegetation classifications are developed for a limited geographic area, usually on the order of a mountain range or basin, and the classification, although made internally consistent, is not often correlated with available regional vegetation data or other classifications. This is analogous to desribing species based on specimens in only one herbarium or museum. If the correlation is completed, rarely is the nomenclature adjusted accordingly. (5) There is no standardized system of nomenclature in wide use in the western U.S. The closest approach to such a system is the system used in habitat type studies supported primarily by the U.S. Forest Service (Pfister 1982). Although there are no formal nomenclatural rules for this system comparable to those of the International Code of Phytosociological Nomenclature (Barkman et al. 1976), correlation efforts have resulted in fairly consistent names. There are also scattered studies in the region that have followed the nomenclatural procedures in the International Code (e.g., Komárková 1976). (6) There is disagreement about whether the classification should be of existing vegetation, potential natural vegetation, presettlement vegetation, or climax vegetation. Also there is no agreement as to whether the latter three of these can be determined, or if they are different. (7) There is no formal agreement on the appropriate level of detail for classifications, though there is wide support for a hierarchy of levels of detail. Finally, (8) though vegetation data have now been collected in the western U.S. for 80 or more years, no one has attempted to systematically revise classifications on a broad scale using a monographic approach, such as is widely and successfully applied in species taxonomy and has been widely used in European syntaxonomy (e.g., Kovář 1981).

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If vegetation varies continuously along environmental gradients, as has been shown by many studies (e.g., Whittaker 1956, Curtis 1959), there may be no unique classification possible, and the situation outlined above may not be subject to remedy. But, as Shimwell (1971) observed, similar concerns have been raised regarding the validity of the taxonomic species concept (Grant 1971), and there is continuing discussion about which attributes (morphological, genetic, biochemical, behavioral, etc.) or combination of attributes should be used to classify individuals into species. One author (Hoog 1981) even suggests that the relevant taxonomic decisions should be left to a committee, who would presumably weigh the evidence and make a majority determination. The need for professional judgment or committee determination in the face of conflicting evidence belies the objectivity of the taxonomic species concept, though it remains a viable global organism classification unit in spite of known deficiencies—probably because of its utility.

There may be compelling biological arguments for not classifying species or vegetation, but the absence of comprehensive detailed vegetation classifications has unfortunate results: (1) While species diversity patterns are beginning to be understood on a general level (Peet et al. 1983), and the contribution of species diversity to stability is being elaborated (Pimm 1984), there have been few studies of the diversity of vegetation units, causes of vegetation diversity, its contribution to landscape stability, or its change over time (but see Romme 1982). (2) There have been few studies examining the distribution and abundance of vegetation units in the landscape. Do landscapes contain common as well as unique vegetation types? How are these dispersed in the landscape? (3) Even less is known about vegetation uniqueness. Can vegetation endemism occur in a region that has low species endemism? (4) Little is known about geographic variation within a particular vegetation unit and what environmental basis there is for the variation (analogous to an ecotype study for a species). Does geographic variation manifest itself in compositional variation, changes in abundance, changes in structure, or some combination (cf Peet 1978)? (5) Can management prescriptions be applied uniformly to all examples of a particular vegetation type? What is the appropriate level of the hierarchy for this to occur? And (6) which vegetation units are being modified by human land uses, which are being irretrievably lost, which are already protected by some means? If individual parts of the vegetation continuum are not named, it is much more difficult to monitor the rate of their loss, or to evaluate their importance for preservation.

The foregoing are among the questions that cannot be addressed effectively without a more systematic classification of vegetation applied over a broad region. Ideally, such a classification would have the following features: (1) a hierarchical system with several levels of detail, (2) within each level of the hierarchy, each unit would encompass a similar amount of variation, (3) standardized nomenclature, (4) a standardized system for revision, and (5) units that are geographically independent. If units are delimited by regions, their total geographic range cannot be studied. In addition, an ideal classification scheme should include a (6) moderately standardized system of data collection, (7) publication of actual stand data, delimitation of type stands, and provision for perpetuation of type stands in natural areas, and (8) classification of presettlement vegetation as much as is still possible, with the closest extant successional stage substituting where no records of presettlement composition and structure remain.

The classification presented here differs from this ideal in several ways. All available stand data on Colorado vegetation (Baker 1983, 1984) are used. These data have been collected in a variety of ways for a variety of purposes. Although it would be desirable to quantitatively analyze this full spectrum of data and objectively divide it into vegetation units, the heterogeneity of data, as well as the size of the matrix that would result, preclude this approach. An effort has been made to define units that encompass similar amounts of variation, but it is not currently possible to evaluate the success of this attempt quantitatively. The classification is not currently a complete hierarchy; only the finest level of the classification, the Plant Association level, is fully developed. Though the Series names listed are in most cases not different from names that have been used in the literature, the Series level presented here is primarily of value as an indexing mechanism. A more meaningful next level for the hierarchy is needed, but its development is beyond the scope of this paper. Most available higher level classificatons (e.g., Brown 1983, UNESCO 1973) have been constructed from the top down and have units that are geographically defined. Although there is value in this approach for many uses, the Plant Associations listed here would overlap several higher level categories in the Brown or UNESCO systems.

For example, the *Agropyron spicatum–Poa sandbergii* grassland is a well-known and internally consistent unit that occurs over a wide geographic range from southern British Columbia in Canada to northern California, and from Montana to central Colorado (see classification for references). This Plant Association would have to be treated in the Brown system by separating it into at least two units, one under the Great Basin Shrub–Grassland Regional Formation, and one under the Rocky Mountain Montane Grassland Regional Formation. To circumvent this problem it would be desirable to modify such systems, or develop new systems that are derived by grouping similar Plant Associations into higher-level units. This development from the bottom up would insure that higher levels of the hierarchy would be additive upward rather than independent classifications at increasingly broad levels.

The classification uses a standardized nomenclature, but this nomenclature has not been developed with a view toward use outside the western U.S. and does not include many features of a needed formal nomenclatural process (Barkman et al. 1976). It is derived largely from general nomenclatural approaches most in use in this region and would require modification to be useful, for example, in regions containing vegetation with species-rich canopies, such as in some forests of the eastern United States. In those regions floristically based nomenclatures are probably more appropriate (cf Braun-Blanquet 1965) and have been widely utilized in similar forests in Europe. Some features of this floristically based approach are used here in vegetation with more species-rich canopies. Though species-rich canopies present nomenclatural problems for dominance-based nomenclatures, species-poor vegetation presents nomenclatural problems for floristically based nomenclatures. It is likey that the two approaches, or perhaps others, will need to be dovetailed if a comprehensive national classification is to be effectively developed in the U.S. On a local basis the data and most of the syntaxa derived by Komárková (1976) using a floristically based approach have been incorporated in this classification with only some nomenclatural adjustment. That such direct conversion is possible attests to the general consistency of the syntaxonomic process up to the point of naming. Though Komárková's names are different, her vegetation units are congruent in level-of-detail and amount of homogeneity with other studies of similar vegetation in Colorado. If this is the case in other parts of the U.S., then developing a national scale classification may be partly a matter of devising a broad nomenclatural process.

It is important to emphasize that the nomenclature does not drive the classification system. Regardless of nomenclatural approach, vegetation units are derived by grouping stands using some set of criteria, perhaps either floristic similarity or similarity in dominants. A name is then applied to the resultant unit. If a stand is then located that has slightly different floristic composition, or different dominants, the stand may be used as the basis for revising the nomenclature of a particular unit, or it may be the basis for additional data collection to determine if a new vegetation unit is warranted. If new data are automatically placed into new units without reference to previously described syntaxa, a proliferation of poorly demarcated syntaxa will result.

The primary purpose of this paper is to sort and revise extant data into a reasonably internally consistent classification that will be useful as a starting point for more quantitative systematic revision. A basic premise of this paper is that methods of classification used in a variety of natural resources taxonomies such as species taxonomy (Hoog 1981), soil taxonomy (USDA Soil Conservation Service 1975), geologic stratigraphy, and others, all utilize similar methodology involving several steps: (1) collection of field data, (2) grouping into taxa, (3) nomenclature, and (4) revision. In the western United States, syntaxonomies are incomplete, not because the process lacks meaning or is more difficult than in other natural resource fields, but because development has not proceeded systematically. Although it will always be possible to develop classifications of the vegetation in the western U.S., the opportunities for classifying vegetation reflecting as nearly as possible presettlement conditions are decreasing as natural vegetation is subjected to increasing land use pressures, and as remnants of the presettlement vegetation spectrum are altered or lost.

METHODS

Approach

The focus of this classification is on the natural vegetation of the state of Colorado. The term *natural* here means the vegetation that existed prior to the changes that have accompanied European settlement, essentially the presettlement vegetation. Excluded from the classification, as a consequence, are newly created vegetation types such as lawns, pastures, gardens, and agricultural fields, or vegetation types that are dominated by exotic species, unless these exotic species now dominate all stands of a particular vegetation type and there is no record of composition prior to the replacement. Currently there are no vegetation types in Colorado that have been completely replaced, so far as I am aware, though there are some vegetation types where the majority of stands are now dominated in the understory by exotics (e.g., *Atriplex confertifolia/Hilaria jamesii*).

The classification does not include only "climax" vegetation types, in the sense used by Daubenmire (1952), because it is likely that large parts of the presettlement landscape contained fire-maintained grasslands and forests or vegetation types whose structure was extensively affected by large native ungulates (e.g., *Bouteloua gracilis* Shortgrass Prairie). These fire and grazing-"disclimaxes" are here considered to be a part of the natural presettlement spectrum and worthy of classification where this is still possible. Much recent evidence (White 1979) suggests that natural disturbances are a part of the natural environmental setting of many kinds of vegetation and may even be promoted by the structure of the vegetation or by the adaptations of its component species. A recently burned but revegetated site, for example, may represent two possible successional states, depending on the natural fire frequency: (1) a state that is compositionally and structurally relatively fixed by recurrent fires, or (2) a state that is temporarily present but will disappear due to a low natural fire frequency and a long period between fires. Though there is a range of possibilities between these extremes, they serve to illustrate the successional perspective taken here. In the first case most stands in the landscape will be in the state common not long after a fire. A few stands will have escaped the average high frequency and perhaps have changed compositionally toward a less fire-adapted structure and composition. In the second case most stands in the landscape will be in a state that develops after a long period without a fire, though a few stands may be in a temporary postfire state.

In the first case, the Association would be described and named based on the most common state, the early postfire state. An example of this would be a fire-maintained montane grassland in Colorado. In the second case the Association would be described and named also based on the most common state, a state after a long period without fire. Other states than those that are the basis for naming would be treated as "Plant Communities," which could be included in the future as a level in the hierarchy under each Plant Association (e.g., Arno 1982). A consequence of this approach is that the number of Plant Associations is finite, but the number of Plant Communities is nearly unlimited, and recently is being dramatically increased as the number of kinds and intensities of human-related environmental effects increases.

This approach assumes a priori knowledge about natural disturbance frequencies that is not completely available, though sufficient information may be available for generalization. General ranges of fire frequencies, for example, have been worked out for the region (Martin 1982) so that we know, for example, that fire return intervals are roughly 5–20 years in dry pine forests and 200–500 years in the subalpine forest. The Plant Associations in subalpine forests would then be described and named based on stands at least 200 years old, and pine forest Associations would be based on stands burned within 20 years. In this context, stands not burned within 20 or so years, if different compositionally, would be considered successional. This approach, though different from Daubenmire's (1952) conception, is implicit in some recent work (e.g., Hess 1981) following that tradition and was suggested in a Working Group report at a workshop on habitat typing in the southwest (Moir and Hendzel 1983). An advantage of this approach is that Plant Associations are real, extant (except where all remnants have been extirpated) kinds of vegetation, rather than a theoretical end point that is seldom reached on most sites due to natural disturbances. In this regard, Daubenmire and Daubenmire (1968:7) remark that "relatively few of our study sites represent climax stands that appear to have reached a completely homeostatic equilibrium."

The Plant Associations in this classification must be considered preliminary because some of the natural disturbance regimes in the region have been altered since settlement. Fire suppression, though, may be less of a factor here than in other areas because, even in dry pine forests here, the natural fire return interval is apparently quite long (Laven et al. 1980); even with suppression, the interval decreased from 66 years prior to settlement to 27 years following initiation of suppression. By the same reasoning, plains Plant Associations that are largely no longer affected by bison or elk grazing must be considered preliminary. Cattle grazing is now prevalent, but cattle differ substantially in diet and grazing behavior from bison (Schwartz and Ellis 1981), with cattle having a more selective diet and spending more time grazing in low areas of the landscape. These differences extended over a long time period would likely result in compositional differences between bison-grazed and cattle-grazed ranges. Although bison-grazed sites are no longer available for sampling, the closest extant successional state would be on sites as free as possible of livestock effects. Extant vegetation on such sites would have to substitute for the presettlement vegetation unless, or until, a natural grazing regime could be reestablished on some sites for study.

The Plant Association is considered here to be a state determined by the prevailing presettlement environmental conditions, including a natural disturbance regime, with some human-related effects. It is primarily a classification unit derived for human purposes, lacking organismic properties, and probably lacking emergent properties. Its primary purpose is for organizing information. It is unlikely that the Plant Associations named here would have retained their composition or structure in perpetuity in the absence of the disturbances associated with settlement. Though the evidence is not extensive, Van Devender and Spaulding (1979) report that the elevational displacement of vegetation associated with the end of the Pleistocene resulted in completely new assemblages. Communities were not simply displaced intact, but were reordered.

This classification does not include only "potential natural vegetation" in the sense used by Küchler (1964) (the vegetation that would result if man were removed from the landscape and the resulting succession telescoped into a short period). Native human cultures, in their use of fire (Moore 1972, Barrett 1980) and their impact on large mammal populations, may have had a significant indirect effect on the structure of many Colorado plant associations since their inception. There is increasing evidence that both human culture and presettlement vegetation in Colorado have a primarily late-Pleistocene or post-Pleistocene origin (Martin and Mehringer 1965, Van Devender and Spaulding 1979). Total removal of humans would likely result in a new kind of vegetation that has never been extant in the region. A premise of the approach aimed at here is that human effects are "natural," in that they have been potentially partly a controlling factor in vegetation development in the region, but European settlement has resulted in a dramatically increased rate of change in the vegetation, accompanied in many cases by wide-scale replacement by agricultural crops or other less-desirable exotic plants, as well as by dramatic changes in structure or composition of many other vegetation types. Although this change is in a sense "natural," the vegetation existing prior to the change is of more than historical interest, because in many cases knowing its composition and structure will be essential if disturbed lands are to be effectively rehabilitated, and if the extinction of the many native plant and animal species poorly adapted to the new cultural vegetation is to be prevented.

This classification is not an integrated classification, combining several attributes of an ecosystem, such as vegetation, soils, and landform, into one system. It is intended to be a classification of the vegetation component of Colorado ecosystems only. An integrated classification system could be developed using this classification for the vegetation component.

Limitations

The classification was developed by sorting actual stand data in the scientific literature identified in Baker (1983, 1984). The classification is preliminary for several reasons: (1) The sorting and evaluating process may result in errors and omissions that can only be corrected with refinement through use and review. (2) Gaps exist in the literature for certain parts of the state (Baker 1982) and for certain kinds of vegetation. Some vegetation types have not been studied in detail and cannot be classified below the Series level. (3) A few new Plant Associations are proposed for the first time here that were not previously described in the literature, but appear reasonable when all available data are examined en masse (e.g., several *Deschampsia* associations). (4) As classifications are completed in other parts of the western U.S., Colorado Associations that extend into those areas may need to be revised. And (5), though stand data were excluded from consideration if disturbance effects were reported or could be inferred, it is possible that a few of the Associations do not represent presettlement conditions. The list should be viewed as a first approximation.

Hierarchical Structure

The classification is structured hierarchically, with four levels of specificity. The upper three levels and the units within them are designed primarily to facilitate organization.

1. System: Overall physiognomy of vegetation. The following are the Systems:
    - Angiosperm Forests/Woodlands
    - Gymnosperm Forests/Woodlands
    - Shrub Associations
    - Grassland Associations
    - Graminoid Associations
    - Herb Associations
2. Cover Class: The dominant genus in the top stratum of the association (e.g., *Pinus*).
3. Series: The dominant species in the top stratum of the association (e.g., *Pinus ponderosa*).
4. Plant Association: This term, which has been widely used in a variety of contexts, is used here to mean a vegetation unit: (1) that is representative of presettlement conditions, (2) that has internal homogeneity in the composition of its component strata (tree, shrub, and herb strata, if present), (3) that is a grouping of several stands, and (4) that has a definable environmental location.

Level of Detail

The definition of a Plant Association above does not specify just how much variation is encompassed in each Association. Though quantitative means have been developed and utilized to define vegetation units within a limited geographic area, objective methods were impractical for this classification. Even with objective methods, only the consequences of choosing a particular level of detail are objectively illustrated. The researcher still must choose the level. Ultimately, the researcher is guided by the purpose for which the classification is designed, or by previous research results and interpretation. This classification extends and modifies the classification method begun by Daubenmire (1952), which has now been completed on many of the National Forests in the western U.S. (Pfister 1982). It is congruent in scale with comparable efforts in Oregon and Washington (Franklin and Dyrness 1973) and Alaska (Viereck and Dyrness 1980). If extended Nationally, classification on this scale would probably result in some 6,000 Plant Associations, assuming about a 250 per state average, and a 50% overlap between states. This level of detail has been used successfully to map vegetation (Komárková and Webber 1979), though, as with soil mapping, some complexes must be used as mapping units. This level of detail is comparable in magnitude to that in soil classification at the Series level, where some 10,500 Series have been described (USDA Soil Conservation Service 1975).

Nomenclature

Development of nomenclature is the final step in classification prior to testing. Nomenclature used here is similar to that used in many studies of vegetation in the western U.S. No formal rules are proposed, but some steps toward standardization are taken. Names used here generally reflect rather closely the composition and structure of the Plant Association, but individual stands may differ somewhat from that composition implied by the name. The range of variation encompassed under a particular name can only be known by consulting the data in the cited references. Although it would be desirable to summarize the variation inherent in each Association, this is beyond the scope of this paper.

Names are generally based on the dominant species (species with the greatest percent canopy cover) in each stratum of most stands of the Association. If a stratum consistently contains co-dominant species (species generally with at least 10% relative cover in a stratum and high constancy in the Association), the most important two or three co-dominants may be included in the name, and are so indicated by being separated by a dash (–). Co-dominants are listed alphabetically within a stratum. If an Association has co-dominants in the top stratum, it would be listed only under the generic name of the first co-dominant (e.g., a *Pinus ponderosa–Pseudotsuga menziesii/Carex rossii* Association would be listed only under PINUS). This nomenclatural approach differs from that of Daubenmire (1952) in that the apparent reproductive potential of the overstory species is not used to determine a potential climax species. If mature, relatively undisturbed stands consistently have co-dominance, that co-dominance is generally recognized here in the nomenclature. Names may occasionally include differential or characteristic species. These are species that are virtually always present, but not necessarily dominant in the Association, though usually absent from related Associations. These species are identified by a star (*) following the species name. Associations are assumed to contain potentially three strata: tree, shrub, and herb. A particular species is here assumed to only belong to one of these strata (e.g., *Picea engelmannii* is always considered a tree, so the shrubby *Picea engelmannii* Associations that characterize krummholz are listed only in the Gymnosperm Forest/Woodland System, not with Shrub Associations). Strata are separated in names by a slash (/). Slashes are not used to separate a dominant from a subdominant. Some associations are heterogenous in a stratum. Their composition may consist of a core species that is always present and an additional species that may be absent from many stands, but that in many stands may be co-dominant with the core species. Because these species lack the high constancy required of a full co-dominant, they are distinguished in names by enclosing them in parentheses (e.g., the *Pinus ponderosa–(Pseudotsuga menziesii)/Carex* *rossii* Association). Physiognomic or environmental descriptors have often been added to names to clarify and add meaning to the name (e.g., *Carex microglochin* Alpine Wetland).

Names listed here may differ substantially, in some instances, from names used in the sources of information cited. This occurs because ecologists use different naming conventions, or may not have incorporated all available data prior to naming. In addition, the standardization applied here results in some new names for some familiar associations. It is hoped that scientists whose work is cited here will understand that this standardization of names and sorting of data is a necessity if a statewide, and eventually a regionwide, classification is to be developed. The nomenclature proposed here may not be the best for such a regionwide classification, but it is intended to illustrate that standardization can be accomplished, and does serve to clarify a proliferation of names for the same vegetation unit.

Species nomenclature generally follows Kartesz and Kartesz (1980). *Agropyron spicatum* var. *inerme* is retained, because it forms grasslands in Colorado that are ecologically very distinct from grasslands formed by *A. spicatum* var. *spicatum*. *Amelanchier* from the same location has been identified as both *A. utahensis* and *A. alnifolia*. Until this taxonomy is resolved, only the name *A. utahensis* is used for all Colorado *Amelanchier*.

Testing

The classification has been under development since 1981 and has been tested in the field during three field seasons. The current classification changed only about 5% from the previous year's version, in spite of about a 10% expansion in the literature and available data. There is no question that additional modification will need to occur as new data accumulate, but it appears unlikely the classification would ever be expanded much beyond about 500 Associations. This is so because new data may just as well result in the alteration of existing Associations as in the creation of new ones. In this sense the classification is not open ended. Additional testing and revision will improve the definition of the Associations listed here, but not necessarily result in many new ones.

Use of the Classification

References pertaining to each Association are listed by number in parentheses following the name. Numbers following "CO:" correspond to the numbered references in two bibliographies of Colorado vegetation description (Baker 1983, 1984). For reference 587 in the Colorado literature, all entries are followed immediately by an additional number. This is the number of the Range Site description. CNHI is included in the list of citations if Colorado Natural Heritage Inventory (CNHI) has additional unpublished data on file. Standard two-letter postal abbreviations indicate literature from adjoining states. These include AZ = Arizona, CA = California, ID = Idaho, IL = Illinois, KS = Kansas, MT/Montana, OK = Oklahoma, OR = Oregon, ND = North Dakota, NE = Nebraska, NM = New Mexico, NV = Nevada, SD = South Dakota, TX = Texas, UT = Utah, WA/Washington, WI = Wisconsin, WY = Wyoming. Numbers following these abbreviations correspond to numbered references listed in the Literature Cited section following the classification. It may on occasion be difficult to locate the actual data in the cited sources because they may be listed under a different name or occur in a data table. A general idea of the range of each Association can be gained by scanning the state abbreviations following the name. It is important to note that the coverage of literature is incomplete, because much unpublished and some published literature was unavailable to me. Coverage is generally best for adjoining states.

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Literature Cited

Arno, S. F. 1982. Classifying forest succession on four habitat types in western Montana. Pages 54–62 *in* J. E. Means, ed., Forest Succession and Stand Development Research in the Northwest, Forestry Sci. Lab., Oregon State Univ., Corvallis. 170 pp.

Baker, W. L. 1982. Vegetation description in Colorado: where are the gaps? J. Colorado-Wyoming Acad. Sci. 14(1):39 (Abstract).

______. 1983. A bibliography of Colorado vegetation description. Great Basin Nat. 43(1):45–64.

______. 1984. Additions to a bibliography of Colorado vegetation description. Great Basin Nat. 44(4):000.

Barkman, J. J., J. Moravec, and S. Rauschert. 1976. Code of phytosociological nomenclature. Vegetatio 32:131–185.

Barrett, S. W. 1980. Indian fires in the pre-settlement forests of western Montana. Pages 35–41 *in* M. A. Stokes, and J. H. Dieterich, tech. coords., Proceedings of the Fire History Workshop [20–24 October 1980, Tucson, Arizona], USDA For. Serv. Gen. Tech. Rep. RM-81, Rocky Mt. For. and Range Exp. Sta., Fort Collins, Colorado. 142 pp.

Braun-Blanquet, J. 1965. Plant Sociology: the study of plant communities. English translation of Pflanzensoziologie by G. D. Fuller and H. S. Conard. Hafner Publ. Co., New York. 439 pp.

Brown, D. E. (ed.) 1983. Biotic communities of the American Southwest–United States and Mexico. Desert Plants 4(1–4):1–342.

Curtis, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. of Wisconsin Press, Madison. 657 pp.

Daubenmire, R. 1952. Forest vegetation of northern Idaho and adjacent Washington, and its bearing on concepts of vegetation classification. Ecol. Monogr. 22:301–330.

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agric. Expt. Sta. Tech. Bull. 60. 104 pp.

Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service Gen. Tech. Rep. PNW-8, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon. 417 pp.

Grant, V. 1971. Plant speciation. Columbia Univ. Press, New York. 435 pp.

Hess, K. 1981. Phyto-edaphic study of habitat types of the Arapaho-Roosevelt National Forest, Colorado. Unpublished dissertation. Colorado State Univ., Fort Collins. 558 pp.

Hoog, G. S. de. 1981. Methodology of taxonomy. Taxon 30:779–783.

Kartesz, J. T., and R. Kartesz. 1980. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Univ. of North Carolina Press, Chapel Hill. 498 pp.

Komárková, V. 1976. Alpine vegetation of the Indian Peaks area, Front Range, Colorado Rocky Mountains. Unpublished dissertation. Univ. of Colorado, Boulder. 655 pp.

Komárková, V., and P. J. Webber. 1978. An alpine vegetation map of Niwot Ridge, Colorado. Arct. and Alpine Res. 10:1–29.

Kovář, P. 1981. The grassland communities of the southeastern basin of the Labe River. 1. Syntaxonomy. Folia Geobot. Phytotax. 16:1–43.

Küchler, A. W. 1964. The potential natural vegetation of the conterminous United States. Amer. Geogr. Soc. Spec. Publ. 361. 116 pp., map.

Laven, R. D., P. N. Omi, J. G. Wyant, and A. S. Pinkerton. 1980. Interpretation of fire scar data from a ponderosa pine ecosystem in the central Rocky Mountains, Colorado. Pages 46–49 *in* M. A. Stokes, and J. Dieterich, tech. coords., Proceedings of the Fire History Workshop [20–24 October 1980, Tucson, Arizona], USDA For. Serv. Gen. Tech. Rep. RM-81, Rocky Mountain For. and Range Exp. Sta., Fort Collins, Colorado.

Martin, P. S., and P. J. Mehringer, Jr. 1965. Pleistocene pollen analysis and biogeography of the southwest. Pages 433–451 *in* H. E. Wright, Jr., and D. G. Frey, eds., The Quaternary of the United States, Princeton Univ. Press, Princeton, New Jersey. 922 pp.

Martin, R. E. 1982. Fire history and its role in succession. Pages 92–99 *in* J. E. Means, ed., Forest succession and stand development research in the Northwest, Forestry Sci. Lab., Oregon State Univ., Corvallis. 170 pp.

Moir, W. H., and L. Hendzel, tech. coord. 1983. Proceedings of the Workshop on Southwestern Habitat Types [6–8 April 1983, Albuquerque, New Mexico], USDA Forest Service, Southwestern Region, Albuquerque, New Mexico. 110 pp.

Moore, C. T. 1972. Man and fire in the central North American grassland 1535–1890: a documentary historical geography. Unpublished dissertation. Univ. of California, Los Angeles. 155 pp.

Peet, R. K. 1978. Latitudinal variation in southern Rocky Mountain forests. J. Biogeog. 5:275–289.

Peet, R. K., D. C. Glenn-Lewin, and J. W. Wolf. 1983. Prediction of man's impact on plant species diversity: a challenge for vegetation science.

Pages 41–54 *in* W. Holzner, M. J. A. Werger, and I. Ikusima, eds., Man's impact on vegetation. Dr. W. Junk Publishers, The Hague.

Pfister, R. D. 1982. Designing succession models to meet management needs. Pages 44–53 *in* J. E. Means, ed., Forest succession and stand development research in the Northwest. Forestry Sci. Lab., Oregon State Univ., Corvallis. 170 pp.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature 307:321–326.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecol. Monogr. 52:199–221.

Schwartz, C. C., and J. E. Ellis. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. J. Appl. Ecol. 18:343–353.

Shimwell, D. W. 1971. The description and classification of vegetation. Univ. of Washington Press, Seattle. 322 pp.

UNESCO. 1973. International classification and mapping of vegetation, Series 6, Ecology and conservation. United Nations Educational, Scientific and Cultural Organization, Paris, France. 93 pp.

USDA Soil Conservation Service. 1975. Soil taxonomy. USDA Agric. Handbk. 436. 754 pp.

Van Devender, T. R., and W. G. Spaulding. 1979. Development of vegetation and climate in the southwestern United States. Science 204:701–710.

Viereck, L. A., and C. T. Dyrness. 1980. A preliminary classification system for vegetation of Alaska. USDA For. Serv. Gen. Tech. Rep. PNW-106, Pacific Northwest Forest and Range Expt. Sta., Portland, Oregon. 38 pp.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. 45:229–299.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26:1–80.

Preliminary Classification of the Natural Vegetation of Colorado

Angiosperm Forests/Woodlands

Acer	
Acer negundo	*Acer negundo* Great Basin Riparian (CO:133, 210; UT:33)
Acer negundo–Populus angustifolia	*Acer negundo–Populus angustifolia/Cornus sericea*° (CO:CNHI)
Alnus	
Alnus incana ssp. *tenuifolia–Betula occidentalis*	*Alnus incana* ssp. *tenuifolia–Betula occidentalis* Montane Riparian (CO:202, 209, 595, 598, 733: WY:112)
Cercocarpus	
Cercocarpus ledifolius	*Cercocarpus ledifolius/Artemisia tridentata* ssp. *wyomingensis–Symphoricarpos oreophilus/Agropyron spicatum* (CO:667)
Populus	
Populus angustifolia	*Populus angustifolia/Amelanchier utahensis* (CO:133, 210, 733)
	Populus angustifolia/Lonicera involucrata (CO:285, 481)
	Populus angustifolia/Salix exigua (CO:36, 133, 209, 266, 458, 648, 733; WY:35, 113)
	Populus angustifolia/Salix scouleriana (CO:334, 656; ID:109)
Populus angustifolia–Populus deltoides ssp. *monilifera–Salix amygdaloides* (CO:36, 85, 575)	
Populus deltoides ssp. *monilifera*	*Populus deltoides* ssp. *monilifera/Distichlis spicata* var. *stricta* (CO:88–91, 116–120, 162, 236–238, 274, 309–316, 330, 364)
	Populus deltoides ssp. *monilifera/Panicum virgatum* (CO:389, CNHI)
Populus deltoides ssp. *monilifera–Salix amygdaloides*	*Populus deltoides* ssp. *monilifera–Salix amygdaloides/Salix exigua/Spartina pectinata*° (CO:89–91, 116–120, 162, 236–238, 311–315)
Populus deltoides ssp. *wislizenii*	*Populus deltoides* ssp. *wislizenii/Rhus trilobata*° (CO:266, 267, 589, CNHI)
Populus tremuloides	*Populus tremuloides/Amelanchier utahensis–Prunus virginiana* var. *melanocarpa–Symphoricarpos oreophilus/Carex geyeri* (CO:59, 157, 213, 271a, 271b, 272, 662, 695)
	Populus tremuloides/Arctostaphylos patula (CO:659)
	Populus tremuloides/Arctostaphylos uva-ursi–Juniperus communis (CO:417, 522, 709)
	Populus tremuloides/Calamagrostis canadensis (CO:391)
	Populus tremuloides/Carex geyeri–Lathyrus leucanthus (CO:50, 173, 209, 213, 272, 355, 695, 733; UT:66, 77; WY:35, 171)
	Populus tremuloides/Ceanothus velutinus° (CO:78, 79)

	Populus tremuloides/Festuca thurberi (CO:107, 111, 209, 210, 301, 413, 506, 522, 540, 733)
	Populus tremuloides/Heracleum sphondylium (CO:59, 78, 79, 210, 213, 272, 355, 695, 733; WY:35, 174)
	Populus tremuloides/Juniperus communis (CO:123, 355; UT:66; WY:35, 174)
	Populus tremuloides/Pteridium aquilinum (CO:78, 79, 213, 385, 392, 695, 733; UT:66; WY:35)
	Populus tremuloides/Rosa woodsii (CO:245, 272; WY:35)
	Populus tremuloides/Rubus parviflorus (CO:59, 78, 355; SD:134; WY:35)
	Populus tremuloides/Symphoricarpos oreophilus/Carex geyeri (CO:59, 210, 540, 571, 662, 681, 695, 733; ID:133)
	Populus tremuloides/Thalictrum fendleri° (CO:59, 78, 79, 209, 210, 213, 272, 301, 675, 695; WY:35, 174)
	Populus tremuloides/Thermopsis divaricarpa (CO:304, 334, 339, 346, 417, 660)
	Populus tremuloides/Veratrum tenuipetalum° (CO:213, 733)

MIXED ANGIOSPERM-GYMNOSPERM FORESTS/WOODLANDS

POPULUS-CONIFER	
Populus angustifolia-Picea pungens (CO:417, 557, 649; WY:35)	*Populus angustifolia-Picea pungens/Alnus incana* ssp. *tenuifolia-Amelanchier utahensis-Salix* ssp. (CO:173, 247)
Populus angustifolia-Pseudotsuga menziesii (CO:356, CNHI)	
Populus tremuloides-Picea pungens (CO:243, 245)	*Populus tremuloides-Picea pungens/Arnica cordifolia* (CO:209, 733; WY:CO REF 733)

GYMNOSPERM FORESTS/WOODLANDS

ABIES	
Abies concolor-Pinus ponderosa-Pseudotsuga menziesii	*Abies concolor-Pinus ponderosa-Pseudotsuga menziesii/Arctostaphylos uva-ursi* (CO:676, 677; AZ:103; NM:CO REF 676, 677)
	Abies concolor-Pinus ponderosa-Pseudotsuga menziesii/Quercus gambelii (CO:676, 677; NM:106)
Abies concolor-Pseudotsuga menziesii	*Abies concolor-Pseudotsuga menziesii/Acer glabrum* (CO:676, 677; AZ:106; NM:106)
	Abies concolor-Pseudotsuga menziesii/Erigeron eximius (CO:676, 677; NM:106, CO REF 676, 677)
	Abies concolor-Pseudotsuga menziesii/Vaccinium sp. (CO:676, 677; NM:CO REF 676, 677)
Abies lasiocarpa	*Abies lasiocarpa/Carex geyeri* (CO:210, 733; ID:77, 133, 138, 139, 152; MT:120; UT:67; WY:35, 36, 139, 171)
Abies lasiocarpa-Picea engelmannii	*Abies lasiocarpa-Picea engelmannii* Ribbon Forest (CO:75, 78, 349, 632; MT:13; ID:13)
	Abies lasiocarpa-Picea engelmannii Tree Island (CO:45, 190, 227, 341, 342, 347–349, 403, 547, 606)
	Abies lasiocarpa-Picea engelmannii/Arnica cordifolia (CO:59, 136, 173, 213, 304, 417; ID:138, 139; MT:120; UT:66; WY:35, 70, 77, 139)
	Abies lasiocarpa-Picea engelmannii/Calamagrostis canadensis (CO:209, 733; ID:133, 138, 139, 152; MT:120; UT:66; WY:35, 36, 139)
	Abies lasiocarpa-Picea engelmannii/Cardamine cordifolia (CO:417, 540, 625, 676, 733)
	Abies lasiocarpa-Picea engelmannii/Carex geyeri (CO:209, 210, 213, 540, 695)
	Abies lasiocarpa-Picea engelmannii/Equisetum arvense (CO:417, 733; ID:138, 139, 152; MT:120; WY:35, 36, 112, 139)
	Abies lasiocarpa-Picea engelmannii/Erigeron eximius (CO:676, 677; NM:CO REF 676, 677)
	Abies lasiocarpa-Picea engelmannii/Linnaea borealis (CO:417, 676, 677, 733; ID:138, 139; MT:120; NM:106; WY:35, 36, 139)

Abies lasiocarpa–Picea engelmannii/Moss (CO:417, 540; NM:CO REF 676, 677; WY:35, 139)
Abies lasiocarpa–Picea engelmannii/Pachistima myrsinites (59, 210, 355, 540, 733)
Abies lasiocarpa–Picea engelmannii/Polemonium delicatum (CO:136, 417, 540, 676, 677, 733; NM:CO REF 676, 677)
Abies lasiocarpa–Picea engelmannii/Ribes lacustre (CO:59, 417)
Abies lasiocarpa–Picea engelmannii/Ribes montigenum (CO:301, 417, 522, 733; ID:138, 139; MT:120; UT:66, 67, 83, 137; WY:35, 36, 139)
Abies lasiocarpa–Picea engelmannii/Ribes wolfii (CO:59, 301)
Abies lasiocarpa–Picea engelmannii/Salix brachycarpa Krummholz (CO:417)
Abies lasiocarpa–Picea engelmannii/Salix glauca Krummholz (CO:209, 210, 733)
Abies lasiocarpa–Picea engelmannii/Senecio triangularis (CO:209, 417, 733)
Abies lasiocarpa–Picea engelmannii/Vaccinium myrtilus (CO:8, 59, 246, 272, 301, 344–346, 355, 417, 733; AZ:106)
Abies lasiocarpa–Picea engelmannii/Vaccinium myrtilus–Vaccinium scoparium (CO:173, 209, 213, 355, 377, 417, 625, 676, 677, 695; AZ:106; NM:106)
Abies lasiocarpa–Picea engelmannii/Vaccinium scoparium (CO:8, 59, 136, 167, 202, 210, 213, 301, 417, 466, 625, 656, 695, 733; AZ:106; ID:77, 133, 138; MT:77, 120; NM:106; OR:53, 55; UT:66, 67, 77, 142; WA:43; WY:35, 36, 70, 77, 114, 128, 129, 139, 171)

JUNIPERUS

Juniperus monosperma–Pinus edulis

Juniperus monosperma–Pinus edulis/Bouteloua curtipendula° (CO:733)
Juniperus monosperma–Pinus edulis/Cercocarpus montanus–Ribes cereum (CO:587N0286)
Juniperus monosperma–Pinus edulis/Quercus × pauciloba° (CO:486, 487; NM:82; OK:19, 131, 162)
Juniperus monosperma–Pinus edulis/Stipa neomexicana (CO:CNHI)
Juniperus monosperma–Pinus edulis/Stipa scribneri (CO:97, 517, 587N0279)

Juniperus osteosperma

Juniperus osteosperma/Agropyron spicatum (CO:667; UT:165; WY:44, 169)
Juniperus osteosperma/Amelanchier utahensis–Philadelphus microphyllus/Elymus salina (CO:CNHI)
Juniperus osteosperma/Elymus salina (CO:662; UT:137)

Juniperus osteosperma–Pinus edulis

Juniperus osteosperma–Pinus edulis/Agropyron smithii (CO:226, 733)
Juniperus osteosperma–Pinus edulis/Agropyron spicatum var. *inerme* (CO:226, 662, 666; UT:137)
Juniperus osteosperma–Pinus edulis/Amelanchier utahensis–Artemisia tridentata ssp. *wyomingensis–Cercocarpus montanus–Symphoricarpos oreophilus/Agropyron spicatum* var. *inerme* (CO:226, 662)
Juniperus osteosperma–Pinus edulis/Amelanchier utahensis–Cercocarpus montanus Marlstone Barren (CO:267, 271a, 662, 666)
Juniperus osteosperma–Pinus edulis/Amelanchier utahensis–Quercus gambelii–Symphoricarpos oreophilus/Carex geyeri (CO:210, 733)
Juniperus osteosperma–Pinus edulis/Artemisia nova/Agropyron spicatum (CO:667; ID:77; UT:140)
Juniperus osteosperma–Pinus edulis/Artemisia nova/Agropyron spicatum var. *inerme* (CO:226, 662)
Juniperus osteosperma–Pinus edulis/Artemisia tridentata ssp. *wyomingensis/Oryzopsis hymenoides–Stipa comata* (226, CNHI)
Juniperus osteosperma–Pinus edulis/Cercocarpus ledifolius var. *intricatus* (CO:659, 667; UT:46)
Juniperus osteosperma–Pinus edulis–Cercocarpus montanus/Agropyron spicatum (CO:667)

	Juniperus osteosperma-Pinus edulis/Cercocarpus montanus/Elymus salina (CO:CNHI)
	Juniperus osteosperma-Pinus edulis/Cercocarpus montanus/Oryzopsis hymenoides (CO:210, 226, 358, 597, 662, 733)
	Juniperus osteosperma-Pinus edulis/Cercocarpus montanus/Poa fendleriana (CO:150, 152, 153, 226)
	Juniperus osteosperma-Pinus edulis/Cercocarpus montanus-Peraphyllum ramosissimum (CO:210, 733)
	Juniperus osteosperma-Pinus edulis/Cowania mexicana (CO:CNHI; UT:111)
	Juniperus osteosperma-Pinus edulis/Hilaria jamesii-Oryzopsis hymenoides-Stipa comata (CO:CNHI)
	Juniperus osteosperma-Pinus edulis/Oryzopsis hymenoides (CO:133, 226, 597, 733)
	Juniperus osteosperma-Pinus edulis/Poa fendleriana (CO:150, 226, 662, 733)
	Juniperus osteosperma-Pinus edulis/Purshia tridentata/Poa fendleriana (CO:150, 153, 226)
	Juniperus osteosperma-Pinus edulis/Quercus gambelii (CO:201, 210, 226, 355, 542, 597, 733)
Juniperus scopulorum	*Juniperus scopulorum/Agropyron spicatum* (CO:552, 564, 689, 733; MT:27; WY:9, 35)
	Juniperus scopulorum/Artemisia tridentata (CO:209, 243, 245, 733; WY:35)
	Juniperus scopulorum/Cercocarpus montanus (CO:209, 733; WY:102)
	Juniperus scopulorum/Muhlenbergia filiculmis (CO:733)
	Juniperus scopulorum/Purshia tridentata (CO:209, 733)
	Juniperus scopulorum/Quercus gambelii (CO:533, 733)
	Juniperus scopulorum-(Pinus flexilis)-(Pinus ponderosa)/Schizachyrium scoparium Scarp Woodland (CO:15, 142, 176, 384, 438, 439, 449, 619-621, CNHI)
PICEA	
Picea engelmannii	*Picea engelmannii/Geum rossii* Krummholz (CO:522; AZ:106, 132; UT:66)
	Picea engelmannii/Trifolium dasyphyllum (CO:167, 209, 417, 733)
Picea engelmannii-Pinus aristata (CO:97, 211, 234, 509, 522, 631)	*Picea engelmannii/Pinus aristata/Festuca thurberi* (CO:676, 677)
Picea pungens	*Picea pungens/Amelanchier utahensis-Cornus sericea/Carex geyeri* (CO:210, 733)
Picea pungens-Pseudotsuga menziesii	*Picea pungens-Pseudotsuga menziesii/Arctostaphylos uva-ursi* (CO:676, 677; NM:106)
	Picea pungens-Pseudotsuga menziesii/Erigeron eximius (CO:676, 677; NM:CO REF 676, 677)
	Picea pungens-Pseudotsuga menziesii/Festuca arizonica (CO:676, 677; NM:CO REF 676, 677)
	Picea pungens-Pseudotsuga menziesii/Linnaea borealis/Carex foenea (CO:676, 677, 733; NM:106)
PINUS	
Pinus aristata	*Pinus aristata/Calamagrostis purpurascens* (CO:733)
	Pinus aristata/Trifolium dasyphyllum (CO:209, 733)
	Pinus aristata-(Pinus ponderosa)-(Pseudotsuga menziesii)/Festuca arizonica-Muhlenbergia montana (CO:522, 548, 676, 677, 733; NM:CO REF 676, 677)
Pinus contorta	*Pinus contorta/Arctostaphylos uva-ursi* (CO:305, 380, 417, 540, 656, 733; OR:53; UT:66, 77; WY:35, 77)
	Pinus contorta/Arctostaphylos uva-ursi-Juniperus communis (CO:8, 305, 339, 380, 417, 522, 554; WY:70, 128)
	Pinus contorta/Carex geyeri (CO:209, 210, 380, 540, 733; ID:77, 138; WY:35, 139, 171)
	Pinus contorta/Juniperus communis (CO:209, 355, 380, 417, 733; WY:35, 44, 128, 139)
	Pinus contorta/Pachistima myrsinites (CO:59, 173, 272, 540, 733)

	Pinus contorta/Shepherdia canadensis° (CO:209, 210, 213, 285, 380, 540, 625, 733; WY:35, 128, 139)
	Pinus contorta/Vaccinium myrtilus (CO:8, 137, 140, 173, 301, 339, 380, 417, 550, 625, 733)
	Pinus contorta/Vaccinium scoparium (CO:202, 209, 355, 733; ID:77, 138; MT:120; OR:55; UT:66; WY:8, 35, 44, 70, 77, 128, 139)
Pinus edulis	*Pinus edulis/Amelanchier utahensis–Arctostaphylos patula–Cercocarpus montanus/Carex pityophila* (CO:662, 666)
	Pinus edulis/Elymus ambiguus (CO:CNHI)
Pinus flexilis	*Pinus flexilis/Arctostaphylos uva-ursi* (CO:676, 677; NM:CO REF 676, 677)
	Pinus flexilis/Calamagrostis purpurascens (CO:209, 417, 733)
	Pinus flexilis/Juniperus communis (CO:140, 165, 209, 213, 417, 660, 733; ID;138, 139; MT:77, 120; WY:35, 44, 77, 139)
	Pinus flexilis/Trifolium dasyphyllum (CO:209, 733)
Pinus ponderosa	*Pinus ponderosa/Carex geyeri* (CO:59, 733; UT:66; WY:35, 171)
	Pinus ponderosa/Carex heliophila (CO:318, 319, 346)
	Pinus ponderosa/Ceanothus fendleri° (CO:417, 554, 595)
	Pinus ponderosa/Cercocarpus montanus/Andropogon gerardii (CO:CNHI)
	Pinus ponderosa/Cercocarpus montanus/Carex rossii (CO:209, 264, 733)
	Pinus ponderosa/Cercocarpus montanus/Muhlenbergia montana (CO:417)
	Pinus ponderosa/Festuca idahoensis (CO:107, 108, 122, 733; ID:138; MT:120; OR:53; UT:66; WY:35, 70)
	Pinus ponderosa/Muhlenbergia montana (CO:106, 209, 417, 676, 677; NM:CO REF 676, 677)
	Pinus ponderosa/Oryzopsis hymenoides (CO:676)
	Pinus ponderosa/Purshia tridentata–Ribes cereum]Muhlenbergia montana (CO:24, 304, 417, 490, 733)
	Pinus ponderosa/Quercus gambelii (CO:16, 78, 201, 207, 210, 355, 417, 508, 533, 542, 733; NM:48, 173; UT:46)
	Pinus ponderosa/Quercus × *pauciloba* (CO:486, 487)
	Pinus ponderosa/Stipa scribneri (CO:CNHI)
	Pinus ponderosa–(Pseudotsuga menziesii)/Arctostaphylos uva-ursi (CO:304, 318, 319, 325, 417, 554, 676, 677; NM:CO REF 676, 677; UT:142; SD-WY:144)
	Pinus ponderosa–(Pseudotsuga menziesii)/Carex rossii (CO:209, 417, 733)
	Pinus ponderosa–(Pseudotsuga menziesii)/Festuca arizonica–Muhlenbergia montana (CO:96, 106–108, 255–261, 522, 530, 560, 676, 677, 733; AZ:34, 57, 103, 110; NM:106)
	Pinus ponderosa–(Pseudotsuga menziesii)/Leucopoa kingii (CO:209, 370, 417, 422, 733)
PSEUDOTSUGA	
Pseudotsuga menziesii	*Pseudotsuga menziesii/Amelanchier utahensis–Quercus gambelii–Symphoricarpos oreophilus/Carex geyeri–Poa fendleriana* (CO:157, 355, 568, 571, 597, 662, 666, 681)
	Pseudotsuga menziesii/Arctostaphylos uva-ursi–Juniperus communis (CO:85, 304, 392, 522, 554, 595, 733; MT:120; WY:CO REF 733)
	Pseudotsuga menziesii/Carex geyeri (CO:59, 173, 209, 733; ID:138; MT:77, 120; UT:66; WY:35)
	Pseudotsuga menziesii/Cercocarpus montanus (CO:733)
	Pseudotsuga menziesii/Juniperus communis (CO:173, 597, 709, 733; ID:77, 138, 139; MT:77, 120; WY:35, 44, 77, 139)
	Pseudotsuga menziesii/Pachistima myrsinites° (CO:78, 210, 213, 695, 733)
	Pseudotsuga menziesii/Quercus gambelii (CO:16, 59, 508, 676, 677, 733)
	Pseudotsuga menziesii/Symphoricarpos oreophilus/Carex geyeri–Poa fendleriana (CO:210, 267, 571, 662, 733)

	Pseudotsuga menziesii–(Pinus ponderosa)/Jamesia americana–Physocarpus monogynus (CO:209, 304, 417, 733)
	Pseudotsuga menziesii–(Pinus ponderosa)/Physocarpus monogynus (CO:14, 209, 417, 733; NM:106; WY:35, 70)

SHRUB ASSOCIATIONS

AMELANCHIER	
Amelanchier utahensis–Artemisia tridentata ssp. *wyomingensis–Cercocarpus montanus–Purshia tridentata–Symphoricarpos oreophilus*	*Amelanchier utahensis–Artemisia tridentata* ssp. *wyomingensis–Cercocarpus montanus–Purshia tridentata–Symphoricarpos oreophilus/Carex geyeri* (CO:271a, 597, 662)
	Amelanchier utahensis–Artemisia tridentata ssp. *wyomingensis–Cercocarpus montanus–Purshia tridentata–Symphoricarpos oreophilus/Oryzopsis hymenoides–Stipa comata* (CO:157, CNHI)
Amelanchier utahensis–Cercocarpus montanus	*Amelanchier utahensis–Cercocarpus montanus/Oryzopsis hymenoides* (CO:597, 662)
Amelanchier utahensis–Symphoricarpos oreophilus	*Amelanchier utahensis–Symphoricarpos oreophilus/Agropyron spicatum* (CO:564, 587N0237, 689)
	Amelanchier utahensis–Symphoricarpos oreophilus/Carex geyeri (CO:597, 662)
ARTEMISIA	
Artemisia arbuscula	*Artemisia arbuscula/Festuca idahoensis* (CO:733; OR:53; WY:35)
Artemisia bigelovii–Frankenia jamesii	*Artemisia bigelovii–Frankenia jamesii/Oryzopsis hymenoides–Stipa neomexicana* (CO:587N058, CNHI)
Artemisia cana	*Artemisia cana/Festuca idahoensis* (CO:733; ID:20, 68, 133; MT:107; WY:20, 35, 108(
	Artemisia cana/Festuca thurberi (CO:209, 564, 578, 689, 733)
Artemisia cana–Purshia tridentata	*Artemisia cana/Purshia tridentata/Stipa comata* (CO:121, 587N0293, CNHI)
Artemisia filifolia	*Artemisia filifolia/Andropogon gerardii* var. *paucipilus–Calamovilfa longifolia–Stipa comata* (CO:1, 106, 124, 125, 135, 154, 180, 486, 487, 503, 518, 527, 587N0016, 587N0019, 733)
Artemisia longiloba	*Artemisia longiloba/Agropyron smithii* (CO:587N0296; WY:35, 153)
	Artemisia longiloba/Agropyron spicatum (CO:485, 562; ID:107; WY:20, 35)
	Artemisia longiloba/Poa sandbergii (CO:564, 689)
Artemisia nova	*Artemisia nova/Agropyron spicatum* (CO:587N0301, 667; CA:4; ID:68, 77, 118, 135; NV:15–17, 20, 175; WY:35, 143, 153)
	Artemisia nova/Stipa comata (CO:667; CA:4; NV:15–17, 20, 175)
Artemisia tridentata ssp. *tridentata*	*Artemisia tridentata* ssp. *tridentata/Agropyron smithii* (CO:268, 552, 564, 689)
	Artemisia tridentata ssp. *tridentata/Elymus cinereus* (CO:209, 587N0285, 662, 667, 733; CA:4; ID:20, 68, 77; NV:18; OR:53, 68; WA:68; WY:20, 35)
	Artemisia tridentata ssp. *tridentata/Hilaria jamesii* (CO:66; CA:4; NM:48, 52; UT:111)
Artemisia tridentata ssp.*tridentata Sarcobatus vermiculatus*	*Artemisia tridentata* ssp. *tridentata–Sarcobatus vermiculatus/Agropyron smithii* (CO:532, 564, 571, 662, 689)
Artemisia tridentata ssp. *vaseyana*	*Artemisia tridentata* ssp. *vaseyana/Agropyron smithii* (CO:532, 562)
	Artemisia tridentata ssp. *vaseyana/Agropyron spicatum* (CO:532, 562, 667; ID:20, 68, 77, 133, 135; MT:20; OR:20, 68; WY:8, 20)
	Artemisia tridentata ssp. *vaseyana/Festuca idahoensis* (CO:209, 210, 532, 552, 562, 689, 733; ID:20, 68, 77, 133, 135, 152; MT:20; NV:93; OR:20, 68; WY:8, 20, 153)
	Artemisia tridentata ssp. *vaseyana/Festuca thurberi* (CO:59, 173, 209, 210, 564, 689, 733)
	Artemisia tridentata ssp. *vaseyana/Leucopoa kingii* (CO:209, 733; WY:35)
	Artemisia tridentata ssp. *vaseyana/Poa fendleriana* (CO:564)
Artemisia tridentata ssp.*vaseyana–Purshia tridentata*	*Artemisia tridentata* ssp. *vaseyana–Purshia tridentata/Agropyron spicatum* (CO:564)

	Artemisia tridentata ssp. *vaseyana–Purshia tridentata/Festuca idahoensis* (CO:564, 689; OR:53; WY:8)
	Artemisia tridentata ssp. *vaseyana–Purshia tridentata/Poa fendleriana* (CO:564)
Artemisia tridentata ssp. *wyomingensis*	*Artemisia tridentata* ssp. *wyomingensis/Agropyron dasystachyum* ssp. *albicans* (CO:173, 187, 358, 733)
	Artemisia tridentata ssp. *wyomingensis/Agropyron smithii* (CO:552, 564, 662, 667, 681, 689)
	Artemisia tridentata ssp. *wyomingensis/Agropyron spicatum* (CO:209, 552, 564, 667, 733; ID:20, 68, 77, 133, 135; MT:20, 107; OR:20, 53, 68; WY:153)
	Artemisia tridentata ssp. *wyomingensis/Elymus ambiguus* (CO:209, 733)
	Artemisia tridentata ssp. *wyomingensis/Stipa comata* (CO:209, 733; CA:4; ID:20, 68, 135; NV:150; OR:53; UT:91; WA:42, 68; WY:35)
	Artemisia tridentata ssp. *wyomingensis/Stipa occidentalis* (CO:564, 689; CA:4; OR:53)
Artemisia tridentata ssp.*wyomingensis–Atriplex confertifolia*	*Artemisia tridentata* ssp. *wyomingensis–Atriplex confertifolia/Elymus salina* (CO:662)
Artemisia tridentata ssp.*wyomingensis–Atriplex confertifolia–Grayia spinosa*°	*Artemisia tridentata* ssp. *wyomingensis–Atriplex confertifolia–Grayia spinosa*°*/Stipa comata* (CO:667)
Artemisia tridentata ssp.*wyomingensis–Purshia tridentata*	*Artemisia tridentata* ssp. *wyomingensis–Purshia tridentata/Agropyron spicatum* (CO:564)
	Artemisia tridentata ssp. *wyomingensis–Purshia tridentata/Stipa comata* (CO:CNHI; CA:4)
Artemisia tridentata ssp.*wyomingensis–Symphoricarpos oreophilus*	*Artemisia tridentata* ssp. *wyomingensis–Symphoricarpos oreophilus/Elymus cinereus* (CO:662, 666)
	Artemisia tridentata ssp. *wyomingensis–Symphoricarpos oreophilus/Oryzopsis hymenoides* (CO:157, 568, 569, 662)
Artemisia tripartita	*Artemisia tripartita/Festuca idahoensis* (CO:209, 733; ID:20, 68, 77, 133, 135, 147; MT:20, 107; WA:20, 42, 68; WY:8, 35, 153)
ATRIPLEX	
Atriplex canescens	*Atriplex canescens/Agropyron smithii–Bouteloua gracilis* (CO:1, 224, 284, 366, 587N09, 587N042, 587N0317)
	Atriplex canescens/Sporobolus airoides (CO:587N034, 587N037; NM:52)
Atriplex confertifolia	*Atriplex confertifolia/Agropyron spicatum* (CO:667)
	Atriplex confertifolia/Agropyron spicatum var. *inerme–Oryzopsis hymenoides* (CO:662, 666)
	Atriplex confertifolia/Elymus salina (CO:571, 662, 667; UT:CNHI)
	Atriplex confertifolia/Hilaria jamesii (CO:66, 67, 135, 324, 587N0401, 587N0404, 587N0406, 587N0410, 588, 589; UT:75, 137, 165–167)
	Atriplex confertifolia/Oryzopsis hymenoides (CO:267, 268, 604, 662; CA:4; NV:12; UT:50, 137, 165)
	Atriplex confertifolia/Sporobolus airoides° (CO:733)
	Atriplex confertifolia/Stipa comata (CO:667)
Atriplex confertifolia–Sarcobatus vermiculatus (CO:239, 266, 267, 597)	
Atriplex corrugata	*Atriplex corrugata* Shale Barren (CO:66, 177, 324, 589; UT:24, 75, 137, 142, 165, 166; WY:35)
Atriplex cuneata–Frankenia jamesii (NM:52)	*Atriplex cuneata–Frankenia jamesii* Shale Barren (CO:CNHI)
Atriplex gardneri	*Atriplex gardneri/Elymus salina* (CO:66, 667; UT:CNHI)
	Atriplex gardneri/Hilaria jamesii (CO:589, 591; UT:75, 166)
	Atriplex gardneri/Oryzopsis hymenoides (CO:667)
CERATOIDES	
Ceratoides lanata	*Ceratoides lanata/Agropyron smithii–Bouteloua gracilis* (CO:587N039, 587N0281)
	Ceratoides lanata/Oryzopsis hymenoides (CO:587N0276; CA:4; NV:12; UT:50)

CERCOCARPUS	
Cercocarpus ledifolius var. *intricatus*	*Cercocarpus ledifolius* var. *intricatus/Agropyron spicatum* (CO:667)
Cercocarpus montanus	*Cercocarpus montanus/Agropyron dasystachyum* ssp. *albicans* (CO:209, 733)
	Cercocarpus montanus/Agropyron spicatum (CO:667, 733; WY:35)
	Cercocarpus montanus/Agropyron spicatum var. *inerme* (CO:662)
	Cercocarpus montanus/Oryzopsis hymenoides (CO:133, 649)
	Cercocarpus montanus/Stipa comata (CO:209, 488, 489, 733)
	Cercocarpus montanus/Stipa occidentalis (CO:733)
Cercocarpus montanus–Rhus trilobata	*Cercocarpus montanus–Rhus trilobata/Andropogon gerardii* (CO:587N0204, CNHI; SD–WY:144)
COLEOGYNE	
Coleogyne ramosissima (General:23)	*Coleogyne ramosissima/Hilaria jamesii* (CO:591; NV:167; UT:99, 167)
CRATAEGUS	
Crataegus douglasii (CO:94, 95)	
Crataegus spp.–mixed (CO:332, 478, 479)	
DRYAS	
Dryas octopetala	*Dryas octopetala/Carex rupestris* (CO:112, 146, 167, 209, 210, 217, 219, 222, 278, 287, 290, 526, 618, 636, 639, 733; WY:35)
OPUNTIA	
Opuntia imbricata (CO:88, 107, 135, 181, 279, 280, 349, 481, 520)	*Opuntia imbricata/Hilaria jamesii* (CO:CNHI)
POTENTILLA	
Potentilla fruticosa (CO:59, 68, 112, 285, 349, 440, 464, 522, 526, 631)	
PURSHIA	
Purshia tridentata	*Purshia tridentata/Muhlenbergia montana* (CO:83, 209, 349, 488, 489, 733)
	Purshia tridentata/Stipa comata (CO:209, 733; CA:4; OR:53; WA:42)
QUERCUS	
Quercus gambelii–Amelanchier utahensis°	*Quercus gambelii–Amelanchier utahensis*°–(*Artemisia tridentata* ssp. *wyomingensis–Cercocarpus montanus–Symphoricarpos oreophilus*)/*Carex geyeri* (CO:157, 271a, 568, 597, 662, 681)
	Quercus gambelii–Amelanchier utahensis°–(*Cercocarpus montanus–Fendlera rupicola–Purshia tridentata–Symphoricarpos oreophilus*)–*Carex geyeri* (CO:134, 150, 201, 508)
	Quercus gambelii–Amelanchier utahensis°–(*Prunus virginiana* var. *melanocarpa–Rosa woodsii–Symphoricarpos oreophilus*)/*Carex geyeri* (CO:150, 210, 213, 587N0238, 597, 662)
Quercus gambelii–Cercocarpus montanus°	*Quercus gambelii–Cercocarpus montanus*°–(*Rhus trilobata*)/*Carex heliophila* (CO:318, 319)
RHUS	
Rhus trilobata–Ribes cereum	*Rhus trilobata–Ribes cereum/Schizachyrium scoparium* (CO:15, 384)
RIBES	
Ribes montigenum	*Ribes montigenum* Alpine Talus (CO:287)
ROBINEA	
Robinea neomexicana (CO:421)	
RUBUS	
Rubus idaeus ssp. *sachalinensis*	*Rubus idaeus* ssp. *sachalinensis* Alpine Scree (CO:287)

SALIX	
Salix arctica–Salix reticulata ssp. *nivalis*	*Salix arctica–Salix reticulata* ssp. *nivalis* Dwarf Alpine Thicket (CO:112, 123, 210, 249, 278, 287, 362, 534, 611, 631, 636, 639; NM:3; UT:92)
Salix bebbiana	*Salix bebbiana* Montane Carr (CO:662; ID:133; UT:46; WY:136, 144)
Salix brachycarpa	*Salix brachycarpa/Carex aquatilis°–Carex rostrata°* Wet Carr (CO:47)
Salix brachycarpa–Salix wolfii–Betula glandulosa°	*Salix brachycarpa–Salix wolfii–Betula glandulosa°/Calamagrostis canadensis* Mesic Carr (CO:47, 285)
Salix exigua	*Salix exigua/Carex* sp. Plains Riparian (CO:236, 238, 314)
Salix geyeriana–Salix lutea	*Salix geyeriana–Salix lutea/Carex rostrata* Wet Carr (CO:733)
Salix geyeriana–Salix monticola	*Salix geyeriana–Salix monticola/Achillea millefolium* ssp. *lanulosa°* Dry Carr (CO:429)
	Salix geyeriana–Salix monticola/Calamagrostis canadensis° Mesic Carr (CO:209, 429, 733; ID:109, 152; WY:35, 113)
Salix glauca	*Salix glauca–(Salix brachycarpa)/Deschampsia cespitosa* Mesic Alpine Thicket (CO:209, 210, 733)
	Salix glauca–(Salix brachycarpa)/Geum rossii Dry Alpine Thicket (CO:206, 522)
Salix glauca–Salix planifolia	*Salix glauca–Salix planifolia* Lacustrine Thicket (CO:112, 250–254; WY:58)
Salix planifolia	*Salix planifolia/Caltha leptosepala* Wet Carr/Alpine Thicket (206, 210, 355, 367, 534, 733)
	Salix planifolia/Carex scopulorum Wet Alpine Thicket (CO:209, 210, 287, 733)
	Salix planifolia/Deschampsia cespitosa Mesic Carr (CO:209, 733)
	Salix planifolia–(Salix brachycarpa)/Deschampsia cespitosa Mesic Alpine Thicket (CO:206; WY:35)
Salix planifolia–Betula glandulosa°–Salix spp.	*Salix planifolia–Betula glandulosa°–Salix* ssp.*/Carex aquatilis°–Carex rostrata°* Wet Carr (CO:209, 429, 733; ID:109, 152; WY:35)
Salix wolfii–Betula glandulosa°–Potentilla fruticosa°	*Salix wolfii–Betula glandulosa°–Potentilla fruticosa°/Achillea millefolium* ssp. *lanulosa°* Dry Carr (CO:47; WY:112)
SARCOBATUS	
Sarcobatus vermiculatus	*Sarcobatus vermiculatus/Distichlis spicata* var. *stricta–(Sporobolus airoides)* (CO:106, 107, 135, 193, 349, 733; CA:4; MT:107; OR:37, 38, 53; WA:42; WY:35, 160)
	Sarcobatus vermiculatus/Suaeda torreyana (CO:66, 355, 589; NV:11; OR:38; UT:50, 165; WY:35)
SYMPHORICARPOS	
Symphoricarpos occidentalis (CO:94, 95, 595, 596; CANADA:41; SD:144; WY:35, 144)	
Symphoricarpos oreophilus	*Symphoricarpos oreophilus/Festuca thurberi* (CO:733)
VACCINIUM	
Vaccinium caespitosum	*Vaccinium caespitosum* Alpine Heath (CO:217, 219, 221, 287, 534; UT:92)
Vaccinium scoparium	*Vaccinium scoparium* Alpine Thicket (CO:45, 287, 403; UT:92)

GRASSLAND ASSOCIATIONS

AGROPYRON	
Agropyron scribneri	*Agropyron scribneri* Alpine Grassland (CO:45, 403, 407, 631)
Agropyron smithii	*Agropyron smithii* Great Basin Grassland (CO:353, 667; AZ:110; NV:104; UT:32, 33)
	Agropyron smithii° Mixed Prairie (CO:63–65, 76, 84, 189, 195, 197–200, 224, 264, 381, 392, 449, 486, 516, 518, 520, 538, 539, 587N01, 587N02, 587N04, 587N08, 587N0202, 587N0208, 592, 593, 596, 609, 733; CANADA:41; KS:65; NE:123; NM:48, CO REF 609; ND:59, 124; OK:28; SD:90; WY:7, 35)
	Agropyron smithii Montane Grassland (CO:443, 446, 458, 515, 576, 587N0233, 587N0243, 587N0247, 587N0257, 587N0317)
	Agropyron smithii Plains Swale Grassland (CO:107, 193, 383, 587N010; CANADA:41; NM:CO REF 609; TX:100; WY:7)

Agropyron spicatum	*Agropyron spicatum–Arenaria hookeri*° (CO:667) *Agropyron spicatum–Bouteloua gracilis* Montane Grassland (CO:564, 689; MT:107) *Agropyron spicatum–Poa fendleriana* Montane Grassland (CO:564, 689, 733; WY:35, 74) *Agropyron spicatum–Poa sandbergii* Palouse Grassland (CO:210, 733; CANADA:145; ID:146; MT:107; OR:53; WA:42; WY:9, 44, 153)
Agropyron spicatum var. *inerme*	*Agropyron spicatum* var. *inerme* Great Basin Grassland (CO:662, 666; UT:60, 73, 117, 121) *Agropyron spicatum* var. *inerme–Oryzopsis hymenoides* Great Basin Grassland (CO:662, 666)
ANDROPOGON	
Andropogon gerardii	*Andropogon gerardii–Bouteloua curtipendula–Bouteloua gracilis–Schizachyrium scoparium* Xeric Tallgrass Prairie (CO:46, 97, 135, 195, 198, 240, 344, 392, 459, 582, 587N053, 587N070, 587N0206, 587N0210, 733; KS:1, 69, 72, 89; NM:CO REF 609; OK:131, 162; WY:63) *Andropogon gerardii–Bouteloua gracilis–Muhlenbergia montana–Schizachyrium scoparium* Xeric Tallgrass Prairie (CO:63–65, 189, 587N0213, 587N0216) *Andropogon gerardii–Panicum virgatum–Schizachyrium scoparium–Sorghastrum nutans* Mesic Tallgrass Prairie (CO:381, 382, 390, 587N036, 587N038, 593, 733; CANADA:96; KS:2, 89; NE:148, 160; OK:19, 28, 29, 64, 81, 126, 130)
Andropogon gerardii var. *paucipilus*	*Andropogon gerardii* var. *paucipilus–Calamovilfa longifolia–Stipa comata* Sandhills Prairie (CO:205, 453, 455, 491, 503, 587N020, 587N022, 733; NE:5, 30, 123, 172; ND:168; WY:35) *Andropogon gerardii* var. *paucipilus–Calamovilfa longifolia–Panicum virgatum–Sorghastrum nutans* Sandhills Tallgrass Prairie (CO:587N029, 587N031, CNH1)
BOUTELOUA	
Bouteloua gracilis	*Bouteloua gracilis* Shortgrass Prairie (CO:12, 166, 198, 200, 223, 224, 349, 366, 520, 555, 592, 593, 595, 596, 653, 733) *Bouteloua gracilis–Buchloe dactyloides* Shortgrass Prairie (CO:12, 15, 54, 55, 76, 100, 106, 107, 110, 135, 160, 181, 205, 241, 283, 364, 366, 378, 383, 389, 392, 441, 482, 511, 518, 520, 538, 592, 593, 733; KS:1, 65, 89; NE:122; NM:48; OK:19, 28; WY:35)
CALAMAGROSTIS	
Calamagrostis canadensis	*Calamagrostis canadensis* Wetland (CO:188, 287, 391, 392, 646; CANADA:96; ID:109; NE:148; WY:35)
CALAMOVILFA	
Calamovilfa longifolia	*Calamovilfa longifolia* Sandhills Prairie (CO:455, CNH1; NE:80, 123, 148; WY:35)
DANTHONIA	
Danthonia intermedia	*Danthonia intermedia–Deschampsia cespitosa* Alpine Grassland (CO:146, 202; UT:115) *Danthonia intermedia–Sibbaldia procumbens*° Alpine Grassland (CO:219, 287, 290, 354, 733) *Danthonia intermedia–Solidago multiradiata*° Subalpine Grassland (CO:210, 733)
Danthonia parryi	*Danthonia parryi* Montane Grassland (CO:209, 443, 444, 473, 483, 581, 733; CANADA:96)
DESCHAMPSIA	
Deschampsia cespitosa	*Deschampsia cespitosa–Achillea millefolium* ssp. *lanulosa*° Dry-mesic Alpine Meadow (CO:52, 56, 400, 409, 522) *Deschampsia cespitosa–Caltha leptosepala*° Very Wet Meadow (CO:52, 56, 209, 210, 249, 367, 407, 646, 733) *Deschampsia cespitosa–Carex nebrascensis*° Wet Montane Meadow (CO:587N0241, 587N0315)

	Deschampsia cespitosa–Geum rossii Wet Alpine Meadow (CO:52, 56, 146, 155, 209, 210, 217, 219–222, 249, 367, 534, 618, 633, 733; UT:92)
	Deschampsia cespitosa–Ligusticum tenuifolium Snow Glade (CO:75)
	Deschampsia cespitosa–Potentilla diversifolia° Mesic Alpine Meadow (CO:52, 56)
Distichlis	
Distichlis spicata var. *stricta*	*Distichlis spicata* var. *stricta* Salt Meadow (CO:458, 515, 583, 584, 587N0314; CANADA:47, 97; KS:155, 156; NE:126, 148, 159; NV:11, 24, 104; ND:127, 168; OK:157; OR:38; UT:21, 24, 51, 116; WA:42)
	Distichlis spicata var. *stricta–Sporobolus airoides–(Agropyron smithii)* Salt Meadow (CO:106, 107, 117, 126, 135, 177, 224, 284, 311, 318, 331, 405, 486, 487, 538, 585, 587N035, 587N0261, 587N0263, 587N0265, 587N0266, 587N0267, 593, 609, 733; KS:54, 89, 155; NM:CO REF 609; OK:119, 157; UT:21, 51; WY:35)
Elymus	
Elymus ambiguus	*Elymus ambiguus* Montane Grassland (CO:97, 209, 733)
Elymus cinereus	*Elymus cinereus* Great Basin Grassland (CO:1, 157, 568, 587N0245, 597, 598, 662, 733; MT:107; UT:33, 73, 141, 161; WA:42; WY:35)
Festuca	
Festuca arizonica	*Festuca arizonica–Festuca thurberi* Montane Grassland (CO:733)
	Festuca arizonica–Muhlenbergia filiculmis Montane Grassland (CO:522, 548)
	Festuca arizonica–Muhlenbergia montane Montane Grassland (CO:96, 122, 256, 257, 259–261, 379, 515, 522, 530, 548, 576, 587N0222, 587N0228, 587N0230, 587N0311, 733; AZ:132; NM:48)
Festuca idahoensis	*Festuca idahoensis* Alpine Grassland (CO:249)
	Festuca idahoensis–Agropyron trachycaulum° Montane Grassland (CO:210, 733; ID:152; MT:107; WY:35, 153)
	Festuca idahoensis–Festuca thurberi Montane Grassland (CO:50, 71, 202, 210, 285, 413, 579, 600, 733)
Festuca thurberi	*Festuca thurberi* Subalpine Grassland (CO:59, 111, 135, 173, 209, 210, 249, 253, 272, 281, 282, 285, 299, 301, 373, 385, 412, 414, 415, 458, 496, 572, 579, 587N0250; NM:3, 105)
Hilaria	
Hilaria jamesii	*Hilaria jamesii* Great Basin Grassland (CO:86, 208, 355, 591; AZ:110; NM:48, 52, CO REF 609; UT:86, 140; WY:35)
	Hilaria jamesii° Mixed Prairie (CO:107, 486, 587N06, 733; NM:CO REF 609; OK:162; TX:100)
	Hilaria jamesii–Oryzopsis hymenoides–Stipa comata Great Basin Grassland (CO:CNHI; UT:84–87, 140)
Hordeum	
Hordeum jubatum	*Hordeum jubatum* Plains Grassland (CO:474, 585, 593; CANADA:47, 97; KS:156; NE:159; ND:127, 168; UT:51, 116)
Muhlenbergia	
Muhlenbergia asperifolia	*Muhlenbergia asperifolia* Salt Meadow (CO:474, 589; UT:21, 46)
Muhlenbergia filiculmis	*Muhlenbergia filiculmis* Montane Grassland (CO:458, 522, 548, 733)
Muhlenbergia montana	*Muhlenbergia montana* Montane Grassland (CO:322, 323, 334, 442–444, 474, 515, 733; AZ:103)
	Muhlenbergia montana–Stipa comata Montane Grassland (CO:31, 83, 161, 209, 392, 733)
Muhlenbergia pungens	*Muhlenbergia pungens* Sandhill Mixed Grassland (CO:455, CNHI; NE:30, 80, 122, 123, 148)
Muhlenbergia torreyi	*Muhlenbergia torreyi* Shortgrass Prairie (CO:12, 100, 107, 516)

ORYZOPSIS	
Oryzopsis hymenoides	*Oryzopsis hymenoides* Shale Barren (CO:552, 564, 689, CNHI) *Oryzopsis hymenoides–Psoralea lanceolata*° Loose Sand Grassland (CO:349, 450, 453, 455, 458; UT:22, 31) *Oryzopsis hymenoides–Stipa comata* Montane Grassland (CO:587N0273, 587N0275, 587N0282; UT:73, 141; WY:35)
PHIPPSIA	
Phippsia algida	*Phippsia algida* Alpine Grassland (CO:CNHI; WY:35)
PHRAGMITES	
Phragmites australis	*Phragmites australis* Wetland (CO:662; CANADA:97, 101; NE:123, 148; ND:45, 127; UT:21; WY:35)
POA	
Poa arctica ssp. *grayana*	*Poa arctica* ssp. *grayana* Alpine Grassland (CO:287)
Poa fendleriana	*Poa fendleriana* Alpine Grassland (CO:321, 400, 401)
Poa lettermanii	*Poa lettermanii* Alpine Grassland (CO:287)
Poa rupicola	*Poa rupicola* Alpine Grassland (CO:403, 636)
PUCCINELLIA	
Puccinellia nuttalliana	*Puccinellia nuttalliana* Salt Meadow (CO:583, 585; CANADA:47, 97, 101; UT:51; WY:35; GENERAL:158)
REDFIELDIA	
Redfieldia flexuosa	*Redfieldia flexuosa* Sandhills Blowout Grassland (CO:449, 518; NE:30, 80, 122, 123, 148; WY:35)
SCHIZACHYRIUM	
Schizachyrium scoparium	*Schizachyrium scoparium* Loess Prairie (CO:12, 15, 284, 390, 587N051, 587N052, CNHI; KS:71, 149) *Schizachyrium scoparium*° Mixed Prairie (CO:195, 198, 318, 320, 516, 587N056, 587N060, 587N062, 587N063, 592, 593, 733; IL:49; KS:1, 65, 89; NE:62; ND:59, 125; OK:28; SD:144; WY:35, 144) *Schizachyrium scoparium* Sandhills Prairie (CO:1, 106, 154, 518, CNHI: NE:80, 122, 123, 142) *Schizachyrium scoparium–Eriogonum flavum*° (CO:CNHI; CANADA:95)
SPARTINA	
Spartina gracilis	*Spartina gracilis* Salt Meadow (CO:193, CNHI; CANADA:97; UT:21; WA:42, 53)
SPOROBOLUS	
Sporobolus airoides	*Sporobolus airoides* Salt Meadow (CO:311, 585, 587N046, 587N047, 733; NM:52)
Sporobolus heterolepis	*Sporobolus heterolepis* Tallgrass Prairie (CO:318, 320; IA:26; NE:164; ND:125; WY:35)
STIPA	
Stipa comata	*Stipa comata*° Mixed Prairie (CO:1, 15, 99, 194, 195, 198, 318, 381, 539, 575, 593, 609; CANADA:41, 95; MT:107; NE:62, 123; ND:59, 124, 125; OK:19, 28; WY:35) *Stipa comata* Montane Grassland (CO:209, 443, 733)
Stipa neomexicana	*Stipa neomexicana*° Mixed Prairie (CO:381, CNHI; NM:6)
Stipa spartea	*Stipa spartea* Tallgrass Prairie (CO:46, 318, 320; CANADA:170; NE:164; ND:125)
Stipa viridula	*Stipa viridula* Plains Grassland (CO:592, 609; CANADA:96)

GRAMINOID ASSOCIATIONS

CAREX	
Carex aquatilis	*Carex aquatilis* Wetland (CO:47, 78, 112, 173, 250–254, 287, 445, 448, 483, 667, 733; CANADA:98; ID:109; OK:119; UT:92; WY:14, 88)
	Carex aquatilis–Carex rostrata Wetland (CO:47, 209, 210, 253, 301, 646, 733; ID:109, 152; WY:58, 112)
Carex arapahoensis	*Carex arapahoensis* Alpine Talus (CO:287, 534, 733)
Carex bipartita	*Carex bipartita* Alpine Wetland (CO:287)
Carex ebenea	*Carex ebenea* Wetland (CO:400, 401, 445)
Carex eleocharis	*Carex eleocharis* Montane Turf (CO:443, 445, 446, 458)
Carex elynoides	*Carex elynoides* Alpine Turf (CO:45, 68, 145, 146, 209, 249, 287, 290, 301, 321, 362, 403, 412, 445, 513, 618, 636, 639, 727, 733; NM:3; UT:92; WY:78)
Carex festivella	*Carex festivella* Montane Wetland (CO:168, 445, 458, 483)
Carex foenea	*Carex foenea* Alpine Talus (CO:287, 400, 401, 445, 733)
Carex haydeniana	*Carex haydeniana* Alpine Wetland (CO:287, 733)
Carex illota	*Carex illota* Alpine Wetland (CO:287)
Carex lanuginosa	*Carex lanuginosa* Montane Wetland (CO:391–393, 445, 548)
Carex microglochin	*Carex microglochin* Alpine Wetland (CO:287, 733)
Carex nardina var. *hepburnii*	*Carex nardina* var. *hepburnii* Alpine Talus (CO:287)
Carex nebrascensis	*Carex nebrascensis–Catabrosa aquatica–Juncus balticus* Spring Wetland (CO:662)
	Carex nebrascensis–Juncus balticus Wetland (CO:94, 95, 163, 318, 455; ID:109; UT:40; WY:108, 144)
Carex nelsonii	*Carex nelsonii* Alpine Wetland (CO:278)
Carex nigricans	*Carex nigricans–(Juncus drummondii)* Alpine Wetland (CO:112, 287, 445, 534, 733; ID:133; OR:53)
Carex pachystachya	*Carex pachystachya* Montane Wetland (CO:253, 254, 445)
Carex perglobosa	*Carex perglobosa* Alpine Rock Outcrop (CO:287, 733)
Carex pyrenaica	*Carex pyrenaica* Alpine Wetland (CO:278, 287, 290, 367, 409, 513, 636, 639)
Carex rossii	*Carex rossii* Subalpine Turf (CO:445)
Carex rostrata	*Carex rostrata* Wetland (CO:391–393, 445, 464; CANADA:98; CA:10; ID:109, 133; OR:53; UT:83; WY:108)
Carex rupestris var. *drummondiana*	*Carex rupestris* var. *drummondiana* Alpine Turf (CO:45, 97, 99, 112, 210, 278, 362, 367, 412, 430, 513, 631, 633, 639, 640, 733; NM:3; UT:25, 92)
Carex scopulorum	*Carex scopulorum–Agropyron trachycaulum*° Alpine Wetland (CO:287)
	Carex scopulorum–Caltha leptosepala° Alpine Wetland (CO:97, 210, 367, 409, 513, 633, 636; WY:35)
Carex vernacula	
Carex vernacula Alpine Wetland (CO:287)	
ELEOCHARIS	
Eleocharis acicularis	*Eleocharis acicularis* Montane Wetland (CO:445, 483, 548)
Eleocharis palustris	*Eleocharis palustris* Wetland (CO:147, 163, 391, 393, 445, 458, 539, 548, 667; NV:11; OK:119; WY:35, 113)
Eleocharis pauciflora	*Eleocharis pauciflora* Wetland (CO:287, 646; CA:10; OR:53; WY:35)
JUNCUS	
Juncus balticus	*Juncus balticus* Wetland (CO:163, 209, 391, 467, 548, 733; ID:109, 152; NV:104; UT:21, 39, 40; WY:35, 108, 113)
Juncus drummondii	*Juncus drummondii* Alpine Wetland (CO:45, 287, 290, 362, 403, 409, 513, 534, 636, 639, 733; ID:133)
KOBRESIA	
Kobresia myosuroides	*Kobresia myosuroides–Carex rupestris* var. *drummondiana*° Alpine Turf (CO:68, 278, 287, 636, 639)
	Kobresia myosuroides–Geum rossii° Alpine Turf (CO:68, 112, 146, 155, 209, 210, 346, 367, 407, 522, 534, 633, 639, 733; NM:3; UT:92; WY:35)
	Kobresia myosuroides–Trifolium dasyphyllum Alpine Turf (CO:522, 733)

SCIRPUS	
Scirpus americanus	*Scirpus americanus* Wetland (CO:455, 539; CANADA:96; KS:155, 156; NE:148; NV:11; OK:119; UT:21, 51; WY:35; GENERAL:158)
Scirpus maritimus	*Scirpus maritimus* Wetland (CO:474, 585; CANADA:94, 97; KS:155, 156; NV:11; ND:45; OK:119, 157; UT;21, 51; GENERAL:158)
Scirpus tabernaemontanii (*S. validus*)	*Scirpus tabernaemontanii–Typha latifolia* Wetland (CO:99, 177, 455; OR:53)

HERB ASSOCIATIONS

Aletes	
Aletes anisatus	*Aletes anisatus–Scutellaria brittonii* Gravel Slide (CO:97)
ANTENNARIA	
Antennaria alpina	*Antennaria alpina* Alpine Wetland (CO:287, 733)
AQUILEGIA	
Aquilegia caerulea	*Aquilegia caerulea–Cirsium scopulorum* Alpine Talus (CO:278, 287, 733)
Aquilegia micrantha	*Aquilegia micrantha–Mimulus eastwoodiae* Hanging Gardens (CO:CNHI; UT:99)
ARENARIA	
Arenaria hookeri	*Arenaria hookeri** Barrens (CO:15, 384; NE:123)
ARTEMISIA	
Artemisia arctica ssp. *saxicola*	*Artemisia arctica* ssp. *saxicola* Alpine Meadow (CO:167, 287, 633, 636, 639, 733)
ATHYRIUM	
Athyrium distentifolium	*Athyrium distentifolium* Alpine Talus (CO:287)
CALTHA	
Caltha leptosepala	*Caltha leptosepala* Wetland (CO:9, 287, 522, 526, 534, 612, 631, 646, 733; WY:35)
CARDAMINE	
Cardamine cordifolia	*Cardamine cordifolia* Alpine Wetland (CO:287; UT:46)
CIRSIUM	
Cirsium scopulorum	*Cirsium scopulorum–Polemonium viscosum* Alpine Talus (CO:287, 733)
CLAYTONIA	
Claytonia megarhiza	*Claytonia megarhiza* Alpine Rock Outcrop (CO:278, 287, 321, 494, 733; WY:78)
ERIGERON	
Erigeron peregrinus ssp. *callianthemus*	*Erigeron peregrinus* ssp. *callianthemus–Ligusticum tenuifolium–Trollius laxus* ssp. *albiflorus* Alpine Wetland (CO:287, 733)
GEUM	
Geum rossii	*Geum rossii–Polygonum bistortoides* Alpine Meadow (CO:209, 210, 534, 733) *Geum rossii–Sibbaldia procumbens* Alpine Meadow (CO:44, 45, 135, 146, 409, 534, 618)
HEUCHERA	
Heuchera spp.	*Heuchera bracteata–Heuchera parviflora* var. *nivalis* Alpine Rock Crevice (CO:287, 657, 733)
IVA	
Iva axillaris	*Iva axillaris* Salt Meadow (CO:667; WY:160)

KOENIGIA	
Koenigia islandica	*Koenigia islandica* Alpine Wetland (CO:287, 362, 513, 636, 639)
LEWISIA	
Lewisia pygmaea	*Lewisia pygmaea* Alpine Meadow (CO:287)
LIGUSTICUM	
Ligusticum porteri	*Ligusticum porteri–Lupinus parviflorus* ssp. *myrianthus* Subalpine Meadow (CO:301, 733)
	Ligusticum porteri–Vicia americana Subalpine Meadow (CO:210)
Ligusticum tenuifolium	*Ligusticum tenuifolium–Deschampsia cespitosa*° Snow Glade (CO:75)
MERTENSIA	
Mertensia ciliata	*Mertensia ciliata* Alpine Wetland (CO:287, 733; ID:109; WY:112)
MINUARTIA	
Minuartia obtusiloba	*Minuartia obtusiloba–Paronychia pulvinata–Silene acaulis* var. *subacaulis–Trifolium nanum* Alpine Fellfield (CO:44, 45, 68, 97, 99, 112, 128, 135, 145, 146, 182, 183, 185, 202, 209, 210, 287, 290, 321, 343, 344, 346, 349, 362, 367, 392, 403, 407, 513, 618, 636, 639, 733; NM:3; UT:92; WY:88)
MYRIOPHYLLUM	
Myriophyllum exalbescens	*Myriophyllum exalbescens* Wetland (CO:253, 254; CANADA:101)
NUPHAR	
Nuphar luteum ssp. *polysepalum*	*Nuphar luteum* ssp. *polysepalum* Wetland (CO:349, 464; OK:119)
POLEMONIUM	
Polemonium viscosum	*Polemonium viscosum* Alpine Meadow (CO:403, 636)
POLYGONUM	
Polygonum amphibium	*Polygonum amphibium* Montane Wetland (CO:250–254, 451, 458)
Polygonum viviparum	*Polygonum viviparum–Carex capillaris*° Alpine Wetland (CO:287, 733; CANADA:98)
POTAMOGETON	
Potamogeton filiformis	*Potamogeton filiformis* Montane Wetland (CO:253, 254)
PRIMULA	
Primula parryi	*Primula parryi* Alpine Wetland (CO:287, 409, 526, 733; AZ:132)
RANUNCULUS	
Ranunculus aquatilis	*Ranunculus aquatilis–Callitriche verna*° Montane Wetland (CO:168, 483)
RORIPPA	
Rorippa curvipes var. *alpina*	*Rorippa curvipes* var. *alpina* Alpine Wetland (CO:287)
SALICORNIA	
Salicornia rubra	*Salicornia rubra* Salt Meadow (CO:1, 583–585; CANADA:47, 97, 101; KS:155, 156; NE:123, 159; NV:11, 24; ND:127, 168; UT:24, 51; WY:35)
SAXIFRAGA	
Saxifraga chrysantha	*Saxifraga chrysantha* Alpine Rock Outcrop (CO:278, 287)
Saxifraga odontoloma	*Saxifraga odontoloma* Alpine Wetland (CO:287, 733)
Saxifraga rivularis	*Saxifraga rivularis* Alpine Rock Outcrop (CO:287)
SEDUM	
Sedum spp.	*Sedum integrifolium–Sedum rhodanthum* Alpine Wetland (CO:287, 526)

SENECIO	
Senecio taraxacoides	*Senecio taraxacoides–Oxyria digyna*° Alpine Talus (CO:287)
Senecio triangularis	*Senecio triangularis* Alpine Wetland (CO:287, 733)
SIBBALDIA	
Sibbaldia procumbens	*Sibbaldia procumbens* Alpine Snowbed (CO:68, 249, 278, 287, 290, 321, 344, 346, 354, 362, 367, 392, 403, 409, 513, 636, 639, 727, 733; WY:78, 88) *Sibbaldia procumbens* Snow Glade (CO:75)
SPARGANIUM	
Sparganium emersum	*Sparganium emersum* Wetland (CO:97, 168, 445, 464, 483)
TRIFOLIUM	
Trifolium dasyphyllum	*Trifolium dasyphyllum* Alpine Fellfield (CO:45, 68, 217, 219, 221, 278, 287, 290, 321, 362, 367, 403, 522, 612, 633, 636, 639, 733; NM:3; UT:61)
Trifolium parryi	*Trifolium parryi* Alpine Fellfield (CO:68, 123, 167, 287, 290, 343, 346, 367, 392, 403, 522, 636, 733; UT:61)
TRIGLOCHIN	
Triglochin maritima	*Triglochin maritima* Salt Meadow (CO:583, 585; CANADA:47, 97; UT:21, 51; GENERAL:158)
TYPHA	
Typha domingensis	*Typha domingensis* Wetland (CO:662; AZ:56)
Typha latifolia	*Typha latifolia* Wetland (CO:91, 312, 13, 330, 364; NV:11; ND:45, 79; UT:21; WY:35)

LITERATURE CITED

Numbers preceded by CO correspond to reference numbers listed in the following two publications:

BAKER, W. L. 1983. A bibliography of Colorado vegetation description. Great Basin Nat. 43(1):45–64.

BAKER, W. L. 1984. Additions to a bibliography of Colorado vegetation description. Great Basin Nat. 44(4):00–00.

Numbers preceded by other state abbreviations are listed below:

1. Albertson, F. W. 1937. Ecology of mixed prairie in west central Kansas. Ecol. Monogr. 7:481–547.
2. Anderson, K. L., and C. L. Fly. 1955. Vegetation-soil relationships in Flint Hills bluestem pastures. J. Range Mgmt. 8:163–169.
3. Baker, W. L. 1983. Alpine vegetation of Wheeler Peak, New Mexico, USA: gradient analysis, classification, and biogeography. Arctic and Alp. Res. 15:223–240.
4. Barbour, M. G., and J. Major, eds. 1977. Terrestrial vegetation of California. John Wiley and Sons, New York. 1002 pp.
5. Barnes, P. W., and A. T. Harrison. 1982. Species distribution and community organization in a Nebraska sandhills mixed prairie as influenced by plant/soil-water relationships. Oecologia 52:192–201.
6. Beavis, W. D., J. C. Owens, J. A. Ludwig, and E. W. Huddleston. 1982. Grassland communities of east-central New Mexico and density of the range caterpillar, *Hemileuca oliviae* (Lepidoptera: Saturniidae). Southwest Nat. 27:335–343.
7. Beetle, A. A. 1952. A relic area on the Wyoming shortgrass plains. J. Range Mgmt. 5:141–143.
8. Beetle, A. A. 1961. Range survey in Teton County, Wyoming. Part 1. Ecology of range resources. Univ. of Wyoming, Agric. Expt. Sta. Bull. 376. 38 pp.
9. Beetle, A. A. 1962. Range survey in Teton County, Wyoming. Part 2. Utilization and condition classes. Univ. of Wyoming, Agric. Expt. Sta. Bull. 400. 38 pp.
10. Benedict, N. B. 1983. Plant associations of subalpine meadows, Sequoia National Park, California. Arctic and Alp. Res. 15:383–396.
11. Billings, W. D. 1945. The plant associations of the Carson Desert region, western Nevada. Butler Univ. Bot. Studies 7:89–123.
12. Billings, W. D. 1949. The shadscale vegetation zone of Nevada and eastern California in relation to climate and soil. Amer. Midl. Natur. 42:87–109.
13. Billings, W. D. 1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. Vegetatio 19:192–207.
14. Billings, W. D., and H. A. Mooney. 1959. An apparent frost hummock-sorted polygon cycle in the alpine tundra of Wyoming. Ecology 40:16–20.
15. Blackburn, W. H., R. E. Eckert, Jr., and P. T. Tueller. 1969a. Vegetation and soils of the Cow Creek watershed. Coll. Agric., Univ. of Nevada Bull. R49. 77 pp.
16. Blackburn, W. H., R. E. Eckert, Jr., and P. T. Tueller. 1969b. Vegetation and soils of the Coils Creek watershed. Coll. Agric., Univ. of Nevada Bull. R48. 82 pp.
17. Blackburn, W. H., R. E. Eckert, Jr., and P. T. Tueller. 1969c. Vegetation and soils of the Crane Springs watershed. Coll. Agric., Univ. of Nevada Bull. R55. 63 pp.

18. Blackburn, W. H., R. E. Eckert, Jr., and P. T. Tueller. 1971. Vegetation and soils of the Rock Springs watershed. Coll. Agric., Univ. of Nevada Bull. R83. 115 pp.

19. Blair, W. F., and T. H. Hubbell. 1938. The biotic districts of Oklahoma. Amer. Midl. Natur. 20:425–454.

20. Blaisdell, J. P., R. B. Murray, and E. D. McArthur. 1982. Managing intermountain rangelands. USDA For. Serv. Gen. Tech. Rep. INT-134, Intermt. For. & Range Expt. Sta., Ogden, Utah. 41 pp.

21. Bolen, E. G. 1964. Plant ecology of spring-fed salt marshes in western Utah. Ecol. Monogr. 34:143–166.

22. Bowers, J. E. 1982. The plant ecology of inland dunes in western North America. J. Arid Environ. 5:199–220.

23. Bowns, J. E., and N. E. West. 1976. Blackbrush (*Coleogyne ramosissima*) on southwestern Utah rangelands. Utah Agric. Expt. Sta. Res. Rep. 27. 30 pp.

24. Branson, F. A., R. F. Miller, and I. S. McQueen. 1967. Geographic distribution and factors affecting the distribution of salt desert shrubs in the United States. J. Range Mgmt. 20:287–296.

25. Briggs, G. M., and J. A. MacMahon. 1982. Structure of alpine plant communities near King's Peak, Uinta Mountains, Utah. Great Basin Nat. 42:50–59.

26. Brotherson, J. D., 1983. Species composition, distribution, and phytosociology of Kaslow prairie, a mesic tall-grass prairie in Iowa. Great Basin Nat. 43:137–167.

27. Brown, R. W. 1971. Distribution of plant communities in southeastern Montana badlands. Amer. Midl. Natur. 85:458–477.

28. Bruner, W. E. 1931. The vegetation of Oklahoma. Ecol. Monogr. 1:99–188.

29. Buck, P., and R. W. Kelting. 1962. A survey of the tall-grass prairie in northeastern Oklahoma. Southwest Nat. 7:163–175.

30. Burzlaff, D. F. 1962. A soil and vegetation inventory and analysis of three Nebraska sandhills range sites. Nebraska Agric. Expt. Sta. Res. Bull. 206. 32 pp.

31. Castle, E. S. 1954. The vegetation and its relationship to the dune soils of Kane County, Utah. Unpublished thesis. Brigham Young Univ., Provo, Utah.

32. Christensen, E. M., and H. B. Johnson. 1964. Presettlement vegetation and vegetational change in three valleys in central Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 4(4):1–16.

33. Christensen, E. M., and S. L. Welsh. 1963. Presettlement vegetation of the valleys of western Summit and Wasatch counties, Utah. Proc. Utah Acad. Sci. 40:163–174.

34. Clary, W. P., and H. A. Pearson. 1969. Cattle preferences for forage species in northern Arizona. J. Range Mgmt. 22(2):114–116.

35. Collins, E. I. 1984. Classification of Wyoming plant communities. Wyoming Natural Heritage Program, The Nature Conservancy, Cheyenne, Wyoming.

36. Cooper, S. V. 1975. Forest habitat types of northwestern Wyoming and contiguous portions of Montana and Idaho. Unpublished dissertation. Washington State Univ., Pullman. 190 pp.

37. Copeland, W. N. 1979. Harney Lake Research Natural Area. Suppl. 9 to Franklin, J. F., et al. 1972. Federal Research Natural Areas in Oregon and Washington: a guidebook for scientists and educators. USDA For. Serv., Pacific Northwest For. and Range Expt. Sta., Portland, Oregon. 21 pp.

38. Copeland, W. N., and S. E. Greene. 1982. Stinking Lake Research Natural Area. Suppl. 12 to Franklin, J. F., et al. 1972. Federal Research Natural Areas in Oregon and Washington: a guidebook for scientists and educators. USDA For. Serv., Pacific Northwest For. and Range Expt. Sta., Portland, Oregon. 21 pp.

39. Cottam, W. P. 1929. Man as a biotic factor illustrated by recent floristic and physiographic changes at Mountain Meadows, Washington County, Utah. Ecology 10:361–363.

40. Cottam, W. P., and G. Stewart. 1940. Plant succession as a result of grazing and of meadow dessication by erosion since settlement in 1862. J. For. 38:613–626.

41. Coupland, R. T. 1950. The ecology of mixed prairie in Canada. Ecol. Monogr. 20:271–315.

42. Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agric. Expt. Sta. Tech. Bull. 62. 131 pp.

43. Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agric. Expt. Sta. Tech. Bull. 60. 104 pp.

44. Despain, D. 1973. Vegetation of the Big Horn Mountains, Wyoming, in relation to substrate and climate. Ecol. Monogr. 43:329–355.

45. Dix, R. L., and F. E. Smeins. 1967. The prairie, meadow, and marsh vegetation of Nelson County, North Dakota. Can. J. Bot. 45:21–58.

46. Dixon, H. 1935. Ecological studies on the high plateaus of Utah. Bot. Gaz. 97:272–320.

47. Dodd, J. D., and R. T. Coupland. 1966. Vegetation of saline areas in Saskatchewan. Ecology 47:958–968.

48. Donart, G. B., D. Sylvester, and W. Hickey. 1978. A vegetation classification system for New Mexico, USA Pages 488–490 *in* D. N. Hyder, ed., Proc. 1st Intern. Rangeland Congr., Denver, Colorado, 14–18 August 1978, Soc. Range Mgmt., Denver, Colorado.

49. Evers, R. A. 1955. Hill prairies of Illinois. Ill. Natur. Hist. Surv. Bull. 26:367–374.

50. Fautin, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecol. Monogr. 16:251–310.

51. Flowers, S. 1934. Vegetation of the Great Salt Lake region. Bot. Gaz. 95:353–418.

52. Francis, R. E., and E. F. Aldon. 1983. Preliminary habitat types of a semiarid grassland. Pages 62–66 *in* W. H. Moir, and L. Hendzel, tech. coord., Proceedings of the Workshop on Southwestern Habitat Types. USDA For. Serv., Southwestern Region, Albuquerque, New Mexico.

53. Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, Pacific Northwest For. and Range Exp. Sta., Portland, Oregon. 417 pp.

54. Geskink, R. W., G. W. Tomanek, and G. K. Hulett. 1970. A descriptive survey of wood phreatophytes along the Arkansas River in Kansas. Trans. Kans. Acad. Sci. 73(1):55–69.

55. Greene, S. E. 1983. Indian Creek Research Natural Area. Suppl. 14 to Federal Research Natural Areas in Oregon and Washington: a guidebook for scientists and educators, by J. F. Franklin, F. C. Hall, C. T. Dyrness,

and C. Maser. Pacific Northwest For. and Range Expt. Sta., Portland, Oregon. 15 pp.

56. Haase, E. F. 1972. Survey of floodplain vegetation along the lower Gila River in southwestern Arizona. J. Ariz. Acad. Sci. 7:75–81.

57. Hanks, J. P., E. L. Fitzhugh, and S. R. Hanks. 1983. A habitat type classification system for ponderosa pine forests of northern Arizona. USDA For. Serv. Gen. Tech. Rep. RM-97, Rocky Mt. For. and Range Exp. Sta., Fort Collins, Colorado. 22 pp.

58. Hanna, L. A. 1934. The major plant communities of the headwater area of the Little Laramie River, Wyoming. Univ. of Wyom., Publ. in Sci., Botany 1:243–266.

59. Hanson, H. C., and W. Whitman. 1938. Characteristics of major grassland types in western North Dakota. Ecol. Monogr. 8:57–114.

60. Hanson, W. R., and L. A. Stoddart. 1940. Effects of grazing upon bunch wheat grass. J. Amer. Soc. Agron. 32:278–289.

61. Harper, K. T., W. K. Ostler, K. B. McKnight, and D. L. Hunter. 1981. Effects of late-lying snow on an alpine herbland in the Uinta Mountains. Pages 179–203 *in* K. T. Harper, ed., Potential ecological impacts of snowpack augmentation in the Uinta Mountains, Utah. Report for Utah Div. Wat. Resources, and Water and Power Resources Serv., by Dept. Botany & Range Sci., Brigham Young Univ., Provo, Utah.

62. Harrison, A. T. 1980. The Niobrara Valley Preserve: its biogeographic importance and description of its biotic communities. Unpublished report prepared for The Nature Conservancy by the Univ. of Nebr., Lincoln.

63. Harrison, A. T., and E. Limbach. 1974. *Andropogon gerardii*: a native tall grass prairie species in eastern Wyoming. J. Colo.-Wyom. Acad. Sci. 7(5):39 (Abstract).

64. Hefley, H. M. 1937. Ecological studies on the Canadian River floodplain in Cleveland County, Oklahoma. Ecol. Monogr. 7(3):345–402.

65. Heitschmidt, R. K., G. K. Hulett, and G. W. Tomanek. 1970. Vegetational map and community structure of a west central Kansas prairie. Southwest Nat. 14:337–350.

66. Henderson, J. A., R. L. Mauk, D. L. Anderson, T. A. Davis, and T. J. Keck. 1977. Preliminary forest habitat types of the Uinta Mountains, Utah. Dept. of For. and Outdoor Recreation, Utah State Univ., Logan. 94 pp.

67. Henderson, J. A., R. L. Mauk, D. L. Anderson, R. Ketchie, P. Lawton, S. Simon, R. H. Sperger, R. W. Young, and A. Youngblood. 1976. Preliminary forest habitat-types of northwestern Utah and adjacent Idaho. Dept. of For. and Outdoor Recreation, Utah State Univ., Logan. 99 pp.

68. Hironaka, M. 1978. Basic synecological relationships of the Columbia River sagebrush type. Pages 27–32 *in* The Sagebrush Ecosystem: a symposium. Utah State Univ., Coll. of Natur. Resources, Logan.

69. Hladek, K. L., G. K. Hulett, and G. W. Tomanek. 1972. The vegetation of remnant shale-limestone prairies in western Kansas. Southwest Nat. 17(1):1–10.

70. Hoffman, G. R., and R. R. Alexander. 1976. Forest vegetation of the Bighorn Mountains, Wyoming: a habitat type classification. USDA For. Serv. Res. Paper RM-170, Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado. 38 pp.

71. Hulett, G. K., C. D. Sloan, and G. W. Tomanek. 1968. The vegetation of remnant grasslands in the loessial region of northwestern Kansas and southwestern Nebraska. Southwest Nat. 13:377–391.

72. Hulett, G. K., and G. W. Tomanek. 1969. Remnant prairies on the shallow limy range site in north central Kansas. J. Range Mgmt. 22:19–23.

73. Hull, A. C., Jr., and M. K. Hull. 1974. Presettlement vegetation of Cache Valley, Utah and Idaho. J. Range Mgmt. 27:27–29.

74. Hyde, R. M., and A. A. Beetle. 1964. Range survey in Sunlight Basin, Park County, Wyoming. Univ. of Wyoming, Agric. Expt. Sta. Bull. 423. 42 pp.

75. Ibrahim, K. J., N. E. West, and D. L. Goodwin. 1972. Phytosociological characteristics of perennial *Atriplex*-dominated vegetation of southeastern Utah. Vegetatio 24:13–22.

76. Irvine, J. R., and N. E. West. 1979. Riparian tree species distribution and succession along the lower Escalante River, Utah. Southwest Nat. 24(2):331–346.

77. Johnson, J. L., and R. D. Pfister. 1982. A survey of potential ecological natural landmarks of the middle Rocky Mountains. Unpublished report prepared for the National Park Service by Intermt. For. and Range Expt. Sta., Ogden, Utah. 197 pp.

78. Johnson, P. L., and W. D. Billings. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. Ecol. Monogr. 32:105–135.

79. Keammerer, W. R., W. C. Johnson, and R. L. Burgess. 1975. Floristic analysis of the Missouri River bottomland forests in North Dakota. Can. Field Natur. 89:5–19.

80. Keeler, K. H., A. T. Harrison, and L. S. Vescio. 1980. The flora and sandhills prairie communities of Arapaho Prairie, Arthur County, Nebraska. Prairie Nat. 12:65–78.

81. Kelting, R. W. 1954. Effects of moderate grazing on the composition and plant production of a native tallgrass prairie in central Oklahoma. Ecology 35:200–207.

82. Kennedy, K. L. 1983. A habitat type classification of the pinyon-juniper woodlands of the Lincoln National Forest, New Mexico. Pages 54–61 *in* W. H. Moir, and L. Hendzel, tech. coord., Proceedings of the Workshop on Southwestern Habitat Types, USDA For. Serv., Southwestern Region, Albuquerque, New Mexico.

83. Kerr, C. W., and J. A. Henderson. 1979. Upland potential vegetation classification and map for a test area, Manti-LaSal National Forest. App. Rep. 15 *in* J. A. Henderson, L. S. Davis, and E. M. Rydberg, eds., ECOSYM-a classification and information system for wildland resource management. Dept. of For. and Outdoor Recr., Utah State Univ., Logan, Utah. 68 pp.

84. Kleiner, E. F. 1968. Comparative study of grasslands of Canyonlands National Park. Unpublished dissertation. Univ. of Utah, Salt Lake City.

85. Kleiner, E. F. 1983. Successional trends in an ungrazed, arid grassland over a decade. J. Range Mgmt. 36(1):114–118.

86. Kleiner, E. F., and K. T. Harper. 1972. Environment and community organization in grasslands of Canyonlands National Park. Ecol. 53:299–309.

87. Kleiner, E. F., and K. T. Harper. 1977. Occurrence of four major perennial grasses in relation to

edaphic factors in a pristine community. J. Range Mgmt. 30:286–289.

88. Knight, D. H., and J. Thilenius. 1975. Vegetation ecology. Pages 37–59, 99–104 *in* D. H. Knight et al., eds., The Medicine Bow Ecology Project: the potential sensitivity of various ecosystem components to winter precipitation management in the Medicine Bow Mountains, Wyoming. Report to the Office of Atmos. Wat. Res., Bur. of Reclam. by the Univ. of Wyoming, Laramie.

89. Kuchler, A. W. 1974. A new vegetation map of Kansas. Ecology 55:586–604.

90. Larson, F., and W. Whitman. 1942. A comparison of used and unused grassland mesas in the badlands of South Dakota. Ecology 23:438–445.

91. Laycock, W. A., and P. W. Conrad. 1981. Responses of vegetation and cattle to various systems of grazing on seeded and native mountain rangelands in eastern Utah. J. Range Mgmt. 34:52–58.

92. Lewis, M. E. 1970. Alpine rangelands of the Uinta Mountains, Ashley and Wasatch National Forests. USDA Forest Service, Ogden, Utah. 75 pp.

93. Lewis, M. E. 1971. Flora and major plant communities of the Ruby-East Humboldt Mountains, with special emphasis on Lamoille Canyon. Unpublished report, Humboldt National Forest, Region IV, USDA Forest Service. 62 pp.

94. Lieffers, V. J., and J. M. Shay. 1982. Distribution and variation in growth in *Scirpus maritimus* var. *paludosus* on the Canadian prairies. Can. J. Bot. 60:1938–1949.

95. Looman, J. 1980. The vegetation of the Canadian prairie provinces. II. The grasslands, Part 1. Phytocoenologia 8:153–190.

96. Looman, J. 1981a. The vegetation of the Canadian prairie provinces. II. The grasslands, Part 2. Mesic grasslands and meadows. Phytocoenologia 9(1/2):1–26.

97. Looman, J. 1981b. The vegetation of the Canadian prairie provinces. III. Aquatic and semi-aquatic vegetation. Phytocoenologia 9(4):473–497.

98. Looman, J. 1982. The vegetation of the Canadian prairie provinces. III. Aquatic and semi-aquatic vegetation, Part 2: Freshwater marshes and bogs. Phytocoenologia 10(4):401–423.

99. Loope, W. L., and N. E. West. 1979. Vegetation in relation to environments of Canyonlands National Park. Vol. I, Pages 195–199 *in* R. M. Linn, ed., Proc. 1st Conf. Sci. Res. in the Nat. Parks, USDI, National Park Service, Transactions and Proceedings Series 5.

100. Lotspeich, F. B., and M. E. Everhart. 1962. Climate and vegetation as soil forming factors on the Llano Estacado. J. Range Mgmt. 15:134–141.

101. Love, A., and D. Love. 1954. Vegetation of a prairie marsh. Bull. Torr. Bot. Club 81:16–34.

102. Maxwell, M. H., and L. N. Brown. 1968. Ecological distribution of rodents on the High Plains of eastern Wyoming. Southwest Nat. 13(2):143–158.

103. Merkle, J. 1962. Plant communities of the Grand Canyon area, Arizona. Ecology 43(4):698–711.

104. Miller, R. F., F. A. Branson, I. S. McQueen, and C. T. Snyder. 1982. Water relations in soils as related to plant communities in Ruby Valley, Nevada. J. Range Mgmt. 35:462–468.

105. Moir, W. H. 1967. The subalpine tall grass, *Festuca thurberi*, community of Sierra Blanca, New Mexico. Southwest Nat. 12:321–328.

106. Moir, W. H., and J. A. Ludwig. 1979. A classification of spruce-fir and mixed conifer habitat types of Arizona and New Mexico. USDA For. Serv. Res. Paper RM-207, Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado. 47 pp.

107. Mueggler, W. F., and W. L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. USDA For. Serv. Gen. Tech. Rep. INT-66, Intermt. For. and Range Expt. Sta., Ogden, Utah. 154 pp.

108. Mutz, K. M., and R. Graham. 1982. Riparian community type classification: Big Piney Ranger District, Wyoming. Unpublished report prepared for the U.S. For. Serv. Region IV, by Meiiji Resource Consultants, Layton, Utah. 88 pp.

109. Mutz, K. M., and J. Queiroz. 1983. Riparian community classification for the Centennial Mountains and South Fork Salmon River, Idaho. Unpublished report prepared for the U.S. For. Serv., Region IV, by Meiiji Resource Consultants, Layton, Utah. 168 pp.

110. Nichol, A. A. 1937. The natural vegetation of Arizona. Univ. of Arizona, Agric. Expt. Sta. Tech. Bull. 68:177–222.

111. Northcutt, B. E. 1978. The plant ecology of Butler Wash, southeastern Utah. Unpublished thesis. Univ. of Colorado, Boulder. 135 pp.

112. Norton, B. E. 1981. Riparian community classification for the Greys River, Wyoming. Unpublished report prepared for the U.S. For. Serv., Region IV, by the Dept. of Range Sci., Utah State Univ., Logan. 190 pp.

113. Olson, R. A., and W. A. Gerhart. 1982. A physical and biological characterization of riparian habitat and its importance to wildlife in Wyoming. Wyoming Fish and Game Dept., State of Wyoming, Cheyenne. 188 pp.

114. Oosting, H. J., and J. F. Reed. 1952. Virgin spruce-fir of the Medicine Bow Mountains, Wyoming. Ecol. Monogr. 22:69–91.

115. Ostler, W. K., K. T. Harper, and K. B. McKnight. 1981. The effects of late lying snow on a subalpine *Danthonia-Deschampsia-Carex* meadow in Utah. Pages 136–178 *in* K. T. Harper, ed., Potential ecological impacts of snowpack augmentation in the Uinta Mountains, Utah. Unpublished Report prepared for the Utah Div. of Wat. Resources and Water and Power Resources Service, by Dept. of Botany and Range Sci., Brigham Young Univ., Provo, Utah.

116. Pammel, L. H. 1903. Some ecological notes on the vegetation of the Uintah Mountains. Proc. Iowa Acad. Sci. 10:57–68.

117. Passey, H. B., and V. K. Hugie. 1963. Variation in bluebunch wheatgrass in relation to environment and geographic location. Ecology 44:158–161.

118. Passey, H. B., V. K. Hugie, E. W. Williams, and D. E. Ball. 1982. Relationships between soil, plant community, and climate on rangelands of the Intermountain West. USDA Soil Conservation Service Tech. Bull. 1669. 123 pp.

119. Penfound, W. T. 1953. Plant communities of Oklahoma lakes. Ecology 34:561–583.

120. Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest habitat types of Montana. USDA For. Serv. Gen. Tech. Rep. INT-34, Intermt. For. and Range Expt. Sta., Ogden, Utah. 174 pp.

121. Pickford, G. D. 1932. The influence of continued grazing and of promiscuous burning on spring-fall ranges in Utah. Ecology 13:159–171.

122. Pool, R. J. 1913. A study of the vegetation of the sandhills of Nebraska. Minnesota Bot. Studies 4(3):184–312, + figures.

123. Pound, R., and F. E. Clements. 1900. The phytogeography of Nebraska. 2d ed. Univ. of Nebraska, Bot. Surv. of Nebr., Lincoln, Nebraska. 442 pp.

124. Quinnild, C. L., and H. E. Cosby. 1958. Relicts of climax vegetation on two mesas in western North Dakota. Ecology 39:29–32.

125. Ralston, R. D. 1968. The grasslands of the Red River Valley. Unpublished dissertation. Univ. of Saskatchewan, Saskatoon.

126. Ray, R. J. 1959. A phytosociological analysis of the tall-grass prairie in northeastern Oklahoma. Ecology 40:255–261.

127. Redmann, R. E. 1972. Plant communities and soils of an eastern North Dakota prairie. Bull. Torr. Bot. Club 99:65–76.

128. Reed, R. M. 1969. A study of forest vegetation in the Wind River Mountains, Wyoming. Unpublished dissertation. Washington State Univ., Pullman. 77 pp.

129. Reed, R. M. 1976. Coniferous forest habitat types of the Wind River Mountains, Wyoming. Amer. Midl. Natur. 95:159–173.

130. Rice, E. L. 1952. Phytosociological analysis of a tall-grass prairie in Marshall County, Oklahoma. Ecology 33:112–116.

131. Rogers, C. M. 1954. Some botanical studies in the Black Mesa region of Oklahoma. Rhodora 56:205–212.

132. Rominger, J. M., and L. A. Paulik. 1983. A floristic inventory of the plant communities of the San Francisco Peaks Research Natural Area. USDA For. Serv. Gen. Tech. Rep. RM-96, Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado. 9 pp.

133. Schlatterer, E. F. 1972. A preliminary description of plant communities found on the Sawtooth, White Cloud, Boulder, and Pioneer mountains. USDA Forest Service, Intermt. Region, Ogden, Utah. 111 pp.

134. Severson, K. E., and J. F. Thilenius. 1976. Classification of quaking aspen stands in the Black Hills and Bear Lodge Mountains. USDA For. Serv. Res. Paper RM-166, Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado. 24 pp.

135. Sharp, L. A., and K. D. Sanders. 1978. Rangeland resources of Idaho. Univ. of Idaho, Wildl. and Range Expt. Sta. Contr. 141. 74 pp.

136. Shute, D. A. 1981. Classification and ecology of *Salix* (willow) communities in southwestern Wyoming. J. Colo.-Wyom. Acad. Sci. 13(1):15 (Abstract).

137. Shute, D. A., and N. E. West. No date. The application of ECOSYM vegetation classifications to rangelands near Price, Utah. App. Reports 14 and 16 *in* J. A. Henderson, and L. S. Davis, eds., ECOSYM—an ecosystem classification and data storage system for natural resources management. 53 pp.

138. Steele, R., R. D. Pfister, R. A. Ryker, and J. A. Kittams. 1981. Forest habitat types of central Idaho. USDA For. Serv. Gen. Tech. Rep. INT-114, Intermt. For. and Range Expt. Sta., Ogden, Utah. 138 pp.

139. Steele, R., S. V. Cooper, D. M. Ondov, D. W. Roberts, and R. D. Pfister. 1983. Forest habitat types of eastern Idaho–western Wyoming. USDA For. Serv. Gen. Tech. Rep. INT-144, Intermt. For. and Range Exp. Sta., Ogden, Utah. 122 pp.

140. Stewart, G., W. P. Cottam, and S. S. Hutchings. 1940. Influence of unrestricted grazing on northern salt desert plant associations in western Utah. J. Agric. Res. 60:289–316.

141. Stoddart, L. A. 1941. The Palouse grassland association in northern Utah. Ecology 22:158–163.

142. Svihla, R. D. 1932. The ecological distribution of the mammals on the north slope of the Uinta Mountains. Ecol. Monogr. 2:47–73.

143. Thatcher, A. P. 1959. Distribution of sagebrush as related to site differences in Albany County, Wyoming. J. Range Mgmt. 12:55–61.

144. Thilenius, J. F. 1971. Vascular plants of the Black Hills of South Dakota and adjacent Wyoming. USDA For. Serv. Res. Paper RM-71, Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado.

145. Tisdale, E. W. 1947. The grasslands of the southern interior of British Columbia. Ecology 28:346–382.

146. Tisdale, E. W. 1979. A preliminary classification of Snake River Canyon grasslands in Idaho. Univ. of Idaho, For. Wildl. and Range Expt. Sta. Note 32. 8 pp.

147. Tisdale, E. W., M. Hironaka, and M. A. Fosberg. 1965. An area of pristine vegetation in Craters of the Moon National Monument, Idaho. Ecology 46:349–352.

148. Tolstead, W. L. 1942. Vegetation of the northern part of Cherry County, Nebraska. Ecol. Monogr. 12:255–292.

149. Tomanek, G. W., and F. W. Albertson. 1957. Variations in cover, composition, production, and roots of vegetation on two prairies in western Kansas. Ecol. Monogr. 27:267–281.

150. Tueller, P. T., and W. H. Blackburn. 1974. Condition and trend of the big sagebrush/needle and thread habitat type in Nevada. J. Range Mgmt. 27:36–40.

151. Tuhy, J. S. 1981. Stream bottom community classification for the Sawtooth Valley, Idaho. Unpublished thesis. Univ. of Idaho, Moscow. 230 pp.

152. Tuhy, J. S., and S. Jensen. 1982. Riparian classification for the upper Salmon/Middle Fork Salmon River drainages, Idaho. Unpublished report prepared for the U.S. For. Serv., Region IV, by White Horse Associates, Smithfield, Utah.

153. Tweit, S. J., and K. E. Houston. 1980. Grassland and shrubland habitat types of the Shoshone National Forest. Unpublished report on file at the Shoshone Nat. For. Headquarters. 143 pp.

154. Ungar, I. A. 1964. A phytosociological analysis of the Big Salt Marsh, Stafford County, Kansas. Trans. Kansas Acad. Sci. 67:50–64.

155. Ungar, I. A. 1965. An ecological study of the vegetation of the Big Salt Marsh, Stafford County, Kansas. Univ. of Kansas Sci. Bull. 46:1–98.

156. Ungar, I. A. 1967. Vegetation-soil relationships on saline soils in northern Kansas. Amer. Midl. Natur. 78:98–120.

157. Ungar, I. A. 1968. Species-soil relationships on the Great Salt Plains of northern Oklahoma. Amer. Midl. Nat. 80:392–406.

158. Ungar, I. A. 1972. The vegetation of inland saline marshes of North America, north of Mexico. Pages 397–411 *in* E. Van der Maarel, and R. Tuxen, eds., Basic problems and methods in phytosociology. Verlag, Dr. W. Junk N.V., Den Haag.

159. Ungar, I. A., W. Hogan, and M. McClelland. 1969. Plant communities of saline soils at Lincoln, Nebraska. Amer. Midl. Nat. 82:564–577.

160. Vass, A. F., and R. Lang. 1938. Vegetative composition, density, grazing capacity and grazing land values in the Red Desert area. Univ. of Wyoming, Agric. Expt. Sta. Bull. 229. 72 pp.

161. Walker, G. R., and J. D. Brotherson. 1982. Habitat relationships of basin wildrye in the high mountain valleys of central Utah. J. Range Mgmt. 35(5):628–633.

162. Waterfall, U. T. 1949. Some results of a summer's botanizing in Oklahoma. Rhodora 51:18–28.

163. Weaver, J. E. 1960. Comparison of vegetation of Kansas-Nebraska driftless hills and loess plains. Ecology 41:73–88.

164. Weaver, J. E., and T. J. Fitzpatrick. 1934. The prairie. Ecol. Monogr. 4:109–295.

165. Welsh, S. L. 1957. An ecological survey of the vegetation of the Dinosaur National Monument, Utah. Unpublished thesis. Brigham Young Univ., Provo, Utah.

166. West, N. E, and K. I. Ibrahim. 1968. Soil-vegetation relationships in the shadscale zone of southeastern Utah. Ecology 49:445–456.

167. West, N. E., R. T. Moore, K. A. Valentine, L. W. Law, P. R. Ogden, F. C. Pinkney, P. T. Tueller, J. H. Robertson, and A. A. Beetle. 1972. Galleta: taxonomy, ecology, and management of *Hilaria jamesii* on western rangelands. Utah Agric. Expt. Sta. Bull. 487. 38 pp.

168. Whitman, W. C., and M. K. Wali. 1975. Grasslands of North Dakota. Pages 53–73 *in* M. K. Wali, ed., Prairie: A Multiple View. Univ. of North Dakota Press, Grand Forks.

169. Wight, J. R., and H. G. Fisser. 1968. *Juniperus osteosperma* in northwestern Wyoming, their distribution and ecology. Univ. of Wyoming, Agric. Expt. Sta., Sci. Monogr. 7. 31 pp.

170. Wilkinson, K., and E. A. Johnson. 1983. Distribution of prairies and solonetzic soils in the Peace River District, Alberta. Can. J. Bot. 61:1851–1860.

171. Wirsing, J. M., and R. R. Alexander. 1975. Forest habitat types on the Medicine Bow National Forest, southeastern Wyoming: preliminary report. USDA For. Serv. Gen. Tech. Rep. RM-12, Rocky Mt. For. and Range Expt. Sta., Fort Collins, Colorado. 11 pp.

172. Wolfe, C. W. 1973. Effects of fire on a sand hills grassland environment. Proc. Tall Timbers Fire Ecol. Conf. 12:241–255.

173. Wright, H. E., Jr., A. M. Bent, B. S. Hansen, and L. H. Maher, Jr. 1973. Present and past vegetation of the Chuska Mountains, northwestern New Mexico. Geol. Soc. Amer. Bull. 84:1155–1180.

174. Youngblood, A. P., and W. F. Mueggler. 1981. Aspen community types on the Bridger-Teton National Forest in western Wyoming. USDA For. Serv. Res. Paper INT-272, Intermt. For. and Range Expt. Sta., Ogden, Utah. 34 pp.

175. Zamora, B., and P. T. Tueller. 1973. *Artemisia arbuscula*, *A. longiloba*, and *A. nova* habitat types in northern Nevada. Great Basin Nat. 33:225–242.

ADDITIONS TO A BIBLIOGRAPHY OF COLORADO VEGETATION DESCRIPTION

William L. Baker[1]

Abstract.— A list of 80 references to Colorado vegetation description is presented, along with county and subject indexes to the list. This list expands an earlier list (663) to include literature through 1983.

The literature describing vegetation in Colorado is expanding rapidly, with most research occurring in the vicinity of universities and in areas of potential energy development. This latter body of literature consists largely of unpublished technical reports that provide background data for environmental impact statements. Much of this invaluable material is not available to the public, though it may represent the only research ever conducted on the vegetation in some areas of Colorado. Lacking access to some of this literature, this list follows the earlier (663) in reporting most published, but only selected unpublished references to vegetation description in Colorado, with less thorough coverage of related subjects.

Criteria for inclusion in the list, use of indexes, and adequacy of coverage are explained in the earier list. All references not contained in the following subject index to related topics pertain solely to vegetation description. Counties not listed in the County Index had no references.

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[1] Colorado Natural Heritage Inventory, 1550 Lincoln Street, Suite 110, Denver, Colorado 80203.

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  Western Colorado Plateaus: 669, 670, 671, 723

BIBLIOGRAPHY

661. Baker, W. L. 1982a. Vegetation description in Colorado—where are the gaps? J. Colo.-Wyom. Acad. Sci. 14(1):39 (Abstract).

662. Baker, W. L. 1982b. Natural vegetation of the Piceance Basin, Colorado. Appendix D, Pages 1–113 *in* J. S. Peterson, and W. L. Baker, eds., Inventory of the Piceance Basin, Colorado: threatened and endangered plants, plant associations, and the general flora. Unpublished report prepared for the Craig District Office, Bureau of Land Management, Craig, Colorado, by Colorado Natural Heritage Inventory, Denver.

663. Baker, W. L. 1983a. A bibliography of Colorado vegetation description. Great Basin Nat. 43(1):45–64.

664. Baker, W. L. 1983b. A preliminary classification of the natural vegetation of Colorado. Unpublished report, Colorado Natural Heritage Inventory, Denver. 17 pp.

665. Baker, W. L. 1983c. Plant associations of special concern in Colorado. Unpublished report, Colorado Natural Heritage Inventory, Denver. 18 pp.

666. Baker, W. L. 1983d. Some aspects of the presettlement vegetation of the Piceance Basin, Colorado. Great Basin Nat. 43(4):687–699.

667. Baker, W. L. 1983e. Natural vegetation of part of northwestern Moffat County, Colorado. Vol. III, Pages 1–121 *in* J. S. Peterson and W. L. Baker, eds., Inventory of selected areas in Colorado. Unpublished report prepared for the Colorado Natural Areas Program, Dept. of Natur. Resources, Denver, Colorado, by Colorado Natural Heritage Inventory, Denver.

668. Beidleman, R. G. 1957. An annotated check list of the flora and fauna of Dinosaur National Monument. Unpublished report, Dinosaur National Monument, Dinosaur, Colorado.

669. Brandegee, T. S. 1876. The flora of southwestern Colorado. Bull. U.S. Geol. and Geogr. Survey of the Territories II(3):227–248.

670. Brown, D. E., ed. 1982. Biotic communities of the American southwest–United States and Mexico. Desert Plants 4(1–4):1–342.

671. Brown, D. E., and C. H. Lowe. 1980. Biotic communities of the southwest. USDA For. Serv. Gen. Tech. Rep. RM-78, Rocky Mt. For. and Range Exp. Sta., Fort Collins, Colorado. [Map].

672. Bye, R. A., and M. E. Floyd. 1980. Vegetation map of the Dolores Archaeological Project. Dolores Archaeological Project 1980 Report.

673. Camp Dresser & McKee, Inc. 1980. Mount Emmons project transmission line corridor selection studies. Tech. Rep. Vol. No. 8, Appendix Tables D10–D82: Vegetation Stand Sample Tables. Unpublished report prepared for AMAX Environmental Services, Inc., Denver, Colorado, by Camp Dresser & McKee, Inc., Wheat Ridge, Colorado.

674. Clements, F. E. 1920. Plant indicators: the relation of plant communities to process and practice. Carnegie Inst. of Wash. Publ. 290. [Chapter IV. Climax Formations of Western North America].

675. Crouch, G. L. 1983. Effects of commercial clearcutting of aspen on understory vegetation and wildlife habitat values in southwestern Colorado. USDA For. Serv. Res. Paper RM-246, Rocky Mt. For. & Range Exp. Sta., Fort Collins, Colorado. 8 pp.

676. DeVelice, R. L. 1983. Forest vegetation of northern New Mexico and southern Colorado. Unpublished dissertation. New Mexico State Univ., Los Alamos. 191 pp.

677. DeVelice, R. L., and J. A. Ludwig. 1983. Climax forest series of northern New Mexico and southern Colorado. Pages 45–53 *in* W. H. Moir and L. Hendzel, tech. coords., Proceedings of the Workshop on Southwestern Habitat Types [6–8 April 1983, Albuquerque, New Mexico], USDA For. Serv., Southwestern Region, Albuquerque, New Mexico.

678. Doty, C. A. 1982. Effects of Gunnison prairie dogs (*Cynomys gunnisoni gunnisoni*) on vegetation. Unpublished thesis. Colorado State Univ., Fort Collins.

679. Elliot-Fisk, D. L., B. S. Adkins, and J. L. Spaulding. 1983. A re-evaluation of the postglacial vegetation of the Laramie Basin, Wyoming-Colorado. Great Basin Nat. 43(3):377–384.

680. Ellis, S. 1981. Vegetation baseline report: GCC reservoir site and pipeline corridor. Unpublished report prepared for Getty Oil Co., Cities Service Co., and Chevron Shale Oil Co. (GCC Joint Venture) by Environmental Research and Technology, Inc., Fort Collins, Colorado.

681. Ellis, S., and P. Hackney. 1981. Vegetation baseline report: Clear Creek property. Unpublished report prepared for Chevron Shale Oil Company, Denver, Colorado, by Environmental Research and Technology, Inc., Fort Collins, Colorado. 2 Vols.

682. Emerick, J. C., and P. J. Webber. 1982. The effects of augmented winter snow cover on the canopy structure of alpine vegetation. Pages 63–81 *in* J. C. Halfpenny, ed., Ecological studies in the Colorado Alpine: a festschrift for John W. Marr, Univ. of Colorado Inst. of Arctic and Alpine Res. Occas. Paper 37, Boulder.

683. Engle, D. M., C. D. Bonham, and L. E. Bartel. 1983. Ecological characteristics and control of Gambel oak. J. Range Mgmt. 36(3):363–365.

684. Erdman, J. A., C. L. Douglas, and J. W. Marr. 1969. Wetherill Mesa studies: environment of Mesa Verde, Colorado. USDI National Park Serv. Archaeol. Res. Series 7-B. 72 pp.

685. Fischer, N. T., M. S. Toll, A. C. Cully, and L. D. Potter. 1983. Vegetation along Green and Yampa rivers and response to fluctuating water levels, Dinosaur National Monument. Final report to the USDI National Park Serv., Denver, Colorado, by the Biology Dept., Univ. of New Mexico, Albuquerque. 179 pp.

686. Flock, J. W. 1983. Changes in alpine plant communities. J. Colo.-Wyom. Acad. Sci. 15(1):37 (Abstract).

687. Floyd, M. E. 1981. The reproductive biology of two species of Piñon pine in the southwestern United States and northern Mexico. Unpublished dissertation. Univ. of Colorado, Boulder. 269 pp.

688. Floyd, M. E. 1982. The interaction of piñon pine and Gambel oak in plant succession near Dolores, Colorado. Southwest Nat. 27:143–147.

689. Francis, R. E. 1983. Sagebrush-steppe habitat types in northern Colorado: a first approximation. Pages 67–71 *in* W. H. Moir, and L. Hendzel, tech. coords., Proceedings of the Workshop on Southwestern Habitat Types. USDA For. Serv., Southwestern Region, Albuquerque, New Mexico.

690. Goodrich, S., E. Neese, J. S. Peterson, and L. England. 1981. Vascular plants of the Uinta Basin, Utah and Colorado. USDI Bur. of Land Management, Denver, Colorado.

691. Hartman, J., and R. Mitchell. 1979. Plants of Mount Goliath Research Natural Area. Prairie Naturalist 11(2):39–48.

692. Helm, D. 1982. Multivariate analysis of alpine snowpatch vegetation cover near Milner Pass, Rocky Mountain National Park, Colorado, USA Arctic and Alpine Res. 14:87–95.

693. Hess, D. W. 1982. The vegetation of Bent's Old Fort, Colorado: 1846 and 1981. J. Colo.-Wyom. Acad. Sci. 14(1):47 (Abstract).

694. Hess, K., and C. Wasser. 1983. Distributional pattern of high elevation grasslands on the White River Plateau, Colorado. Soc. Range Mgmt. 35th annual meeting, Calgary, Alberta, Abstracts p. 36.

695. Hoffman, G. R., and R. R. Alexander. 1983. Forest vegetation of the White River National Forest in western Colorado: a habitat type classification. USDA For. Serv. Research Paper RM-249. Rocky Mt. For. & Range Exp. Sta., Fort Collins, Colorado. 36 pp.

696. Holmgren, A. H. 1962. The vascular plants of the Green River from Flaming Gorge to Split Mountain Gorge. Unpublished report prepared for Dinosaur National Monument by Utah State Univ., Logan. 40 pp.

697. Holtmeier, F. K. 1981. What does the term "Krummholz" really mean? Observations with special reference to the Alps and the Colorado Front Range. Mt. Res. and Develop. 1(3–4):253–260.

698. Ives, J. D., and K. J. Hansen-Bristow. 1983. Stability and instability of natural and modified upper timberline landscapes in the Colorado Rocky Mountains, USA. Mt. Res. and Develop. 3(2):149–155.

699. Knowles, P., and M. C. Grant. 1983. Age and size structure analyses of Engelmann spruce, ponderosa pine, lodgepole pine, and limber pine in Colorado. Ecology 64(1):1–9.

700. Komárková, V., and H. Gordon. 1982. The recovery of plant communities after disturbance along the Front Range, Colorado. Unpublished report, Colorado Comission on Higher Education, Denver. 271 pp.

701. Lindauer, I. E. 1983. A comparison of the plant communities of the South Platte and Arkansas river drainages in eastern Colorado. Southwest Nat. 28(3):249–259.

702. Lindauer, I. E., C. E. Olmsted, III, W. A. Kelley, and W. F. Grey. 1982. Terrestrial ecosystems of northwest Colorado: an annotated bibliography and vegetation classification. Unpublished report prepared for the State Office, Bureau of Land Management, by Univ. of Northern Colorado, Greeley. 123 pp.

703. Lynch, D. L. 1973. An ecosystem guide for mountain land planning, Level 1. Coll. of For. and Natur. Resources, Colorado State Univ., Fort Collins. 94 pp.

704. MacKay, H. A. 1970. A comparative floristic study of the Rio Hondo Canyon-Lake Fork-Wheeler Peak locale, New Mexico, and the Huerfano River-Blanca Peak locale, Colorado. Unpublished dissertation. Univ. of New Mexico, Albuquerque. 226 pp.

705. Markgraf, V., and L. Scott. 1981. Lower timberline in central Colorado during the past 15,000 years. Geology 9:231–234.

706. May, D. E., and P. J. Webber. 1982. Spatial and temporal variation of the vegetation and its productivity, Niwot Ridge, Colorado. Pages 35–62 *in* J. C. Halfpenny, ed., Ecological studies in the Colorado Alpine: a festschrift for John W. Marr, Univ. of Colorado. Inst. of Arctic and Alpine Research Occas. Paper 37. Boulder.

707. Moir, W. 1971. Tall grass prairies in remnant locations in Boulder and Jefferson counties, Colorado. Unpublished report on file at Colorado Natural Heritage Inventory, Denver.

708. Moore, C. T. 1972. Man and fire in the central North American grassland 1535–1890: a documentary historical geography. Unpublished dissertation, Univ. of California, Los Angeles. 155 pp.

709. Murphy, P. H. 1982. The forest vegetation of the Lost Creek area in the southern Front Range, Colorado. Unpublished thesis. Univ. of Colorado, Boulder. 145 pp.

710. Nichols, H. 1982. Review of Late Quaternary history of vegetation and climate in the mountains of Colorado. Pages 27–33 *in* J. C. Halfpenny, ed., Ecological studies in the Colorado Alpine: a festschrift for John W. Marr, Univ. of Colorado Inst. of Arctic and Alpine Res. Occas. Paper 37, Boulder.

711. Parker, A. J., and K. C. Parker. 1983. Comparative successional roles of trembling aspen and lodgepole pine in the southern Rocky Mountains. Great Basin Nat. 43(3):447–455.

712. Peterson, J. S., and W. L. Baker. 1982. Inventory of the Piceance Basin, Colorado: threatened and endangered plants, plant associations, and the general flora. Unpublished report prepared for the Craig District Office, Bureau of Land Management, Craig, Colorado, by Colorado Natural Heritage Inventory, Denver. 5 vols.

713. Peterson, J. S., and W. L. Baker. 1983a. Inventory of the Piceance Basin, Colorado: threatened and endangered plants, plant associations, and the general flora. J. Colo.-Wyom. Acad. Sci. 15(1):42–43 (Abstract).

714. Peterson, J. S., and W. L. Baker. 1983b. Inventory of selected areas in Colorado. Unpublished report prepared for the Colorado Natural Areas Program, Department of Natural Resources, Denver, Colorado, by Colorado Natural Heritage Inventory, Denver. 3 vols.

715. Phillips, V. D., III. 1982. Responses by alpine plants and soils to microtopography within sorted polygons. Unpublished dissertation. Univ. of Colorado, Boulder. 219 pp.

716. Quinn, J. A. 1974. Factors contributing to the discontinuous distribution of piñon pine in the Front Range of Colorado. Unpublished thesis. Univ. of Colorado, Boulder. 81 pp.

717. Reichhardt, K. L. 1982. Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. Southwest Nat. 27:299–304.

718. Rio Blanco Oil Shale Co. 1975. Progress report 4—summary: tract C-a oil shale development. Gulf Oil Corp. and Standard Oil Co., Denver, Colorado.

719. Rio Blanco Oil Shale Co. 1980. Rio Blanco Oil Shale Company modular development phase monitoring

report 6. Mid-year report, December 1979–May 1980. Rio Blanco Oil Shale Co., Denver, Colorado. 2 vols.

720. Rio Blanco Oil Shale Co. 1981. Rio Blanco Oil Shale Company modular development phase monitoring report 7. Year-end report. December 1979–November 1980. Rio Blanco Oil Shale Co., Denver, Colorado. [Vegetation: Appendix 3-1].

721. Rottman, M. L., and E. L. Hartman. 1982. A floristic study of North Pole Basin, Elk Mountains, Colorado. J. Colo.-Wyom. Acad. Sci. 14(1):39–40 (Abstract).

722. Schmid, J. M., and R. H. Frye. 1977. Spruce beetle in the Rockies. USDA For. Serv. Gen. Tech. Rep. RM-49. Rocky Mt. For. & Range Exp. Sta., Fort Collins, Colorado. 38 pp.

723. Schmidt, R. A., Sr., ed. 1983. Management of cottonwood-willow riparian associations in Colorado. Colorado Chapter, The Wildlife Society. 53 pp.

724. Shantz, H. L. 1905. A study of the vegetation of the mesa region east of Pike's Peak: the *Bouteloua* formation. I. Structure of the formation. II. Development of the formation. Unpublished dissertation. Univ. of Nebraska, Lincoln.

725. Slauson, W. L., C. W. Welden, and R. T. Ward. 1982. Pattern and size relationships in *Pinus edulis* and *Juniperus osteosperma* in northwest Colorado. J. Colo.-Wyom. Acad. Sci. 14(1):31 (Abstract).

726. Somers, L. P., III. 1981. Carbon junction coal mine vegetation study, Pueblo Coal Co., La Plata County, Colorado. Unpublished report prepared by Four Corners Environmental Research Institute, Durango, Colorado. 32 pp.

727. Starr, S. E. 1983. The alpine vegetation of Gold Ridge, Colorado. Unpublished thesis. Western State College, Gunnison, Colorado. 85 pp.

728. Stearns-Roger, Inc. 1970. Site investigations: Hayden and Craig, Colorado. Phase B. Unpublished report prepared for Colorado Ute Electric Assoc., Montrose, Colorado, by Stearns-Roger, Inc., Environmental Sciences Division, Denver, Colorado.

729. Steele, C. S. 1983. Vegetation of the Dakota hogback in Colorado, relative to edaphic factors and slope orientation. J. Colo.-Wyom. Acad. Sci. 15(1):27 (Abstract).

730. Stevens, D. R. 1983. Revegetation of the Ouzel Burn in Rocky Mountain National Park. J. Colo.-Wyom. Acad. Sci. 15(1):25 (Abstract).

731. Turner, G. T. 1971. Soil and grazing influences on a salt-desert shrub range in western Colorado. J. Range Mgmt. 24:31–37.

732. USDA Forest Service. 1979. Region 2: Plant Series Maps. USDA For. Serv. Regional Office, Range, Wildlife, and Ecology, Denver, Colorado.

733. USDA Forest Service. 1983. Plant associations of Region Two. 3d ed. USDA For. Serv., Region Two, Range, Wildlife, and Ecology, Denver, Colorado. 379 pp.

734. USDA Soil Conservation Service. 1976. Land use and natural plant communities-maps. USDA Soil Conserv. Serv., Portland, Oregon.

735. Vale, T. R. 1975. Presettlement vegetation in the sagebrush-grass area of the Intermountain West. J. Range Mgmt. 28:32–36.

736. Weber, W. A. 1964. Botany of the Boulder region. Univ. of Colorado Museum Leaflet 13:43–46.

737. Weber, W. A., V. Siplivinsky, and C. Rector. 1982. A checklist of vascular plants of Mesa County and Colorado National Monument, Univ. of Colorado Herbarium, Boulder. 77 pp,

738. Weber, W. A., J. Wingate, and B. Macleod. 1982. A checklist of vascular plants of Moffat County. Univ. of Colorado Herbarium, Boulder. 65 pp.

739. Welden, C. W. 1982. Pattern in alpine tundra. J. Colo.-Wyom. Acad. Sci. 14(1):31 (Abstract).

740. Williams, G. P. 1978. Historical perspective of the Platte rivers in Nebraska and Colorado. Pages 11–41 *in* W. D. Graul and S. J. Bissell, tech. coords., Lowland River and Stream Habitat in Colorado: a symposium. Colorado Chapter Wildlife Soc. and Colorado Audubon Council, Denver.

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